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THE EFFECTS OF PREDATION AND FOOD ON RED SQUIRREL SURVIVAL DURING A SNOWSHOE HARE DECLINE.

BY

A. KARI STUART-SMITH ©

A thesis submitted the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1993

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE EFFECTS OF PREDATION AND AVAILABILITY OF FOOD ON RED SQUIRREL SURVIVAL DURING A SNOWSHOE HARE DECLINE submitted by A. KARI STUART-SMITH in partial fulfilment of the requirements for the degree of Master of Science.

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April 7, 1993

DEDICATION

This thesis is dedicated to my parents and to my grandparents, whose care and concern for prairie wildlife on their farm instilled a love of wildlife in me.

ABSTRACT

I examined the effects of predation and food on red squirrel (*Tamiasciurus hudsonicus*) survival from Spring 1991 to Autumn 1992 in the south-western Yukon, Canada (61° N, 138° W), during a cyclic decline of snowshoe hares (*Lepus americanus*). There were two main objectives: 1) to determine if predation on red squirrels increased as snowshoe hare densities declined, and if so, if a decrease in red squirrel densities resulted, and 2) to determine if survival of adult red squirrels is affected by the availability and distribution of food.

I monitored survival of adult and juvenile squirrels on a site where mammalian predators were experimentally excluded and on an unmanipulated site (control). There was a significant decrease in adult survivorship on the control from 1991 to 1992, but not on the exclosure. On the control, predation on squirrels doubled from 1991 to 1992. Lower adult survivorship in 1992 was likely due to higher predation pressure caused by the hare decline. Juvenile survivorship was lower than adult survivorship, and similar in both years on both sites. Weather conditions and food availability negatively affected survival of neonates, but not of adults. Population densities on both sites were higher in March 1992 than in March 1991, but density on the control was lower in August 1992 than in August 1991, whereas density on the exclosure was higher in August 1992 than in August 1991. The decrease in density on the control was due almost entirely to predation. To determine the effects of availability and distribution of food on survival I distributed supplemental food (sunflower seeds) in two different ways (exposed to and covered from predators) to individual adult females, and monitored their behaviour and survival. Foraging behaviour varied with the distribution of food, but females provided with supplemental food showed similar survival and weights to adults without supplemental food, regardless of its distribution. Similarly, adult females provided with supplemental food from November 1991 through April 1992 showed similar survival and weight to females without supplemental food during winter. There was no difference in the survival or weights of adult red squirrels on a predator exclosure, food addition, predator exclosure and food addition, and control site from August 1991 through mid-June 1992, or from mid-June through August 1992.

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CHAPTER 1

GENERAL INTRODUCTION TO THE STUDY

Northern boreal and arctic regions are characterized by population cycles of small mammalian herbivores. Voles and lemmings undergo 3-4 year population cycles in Fennoscandia and the Nearctic (Krebs and Myers 1974), while snowshoe hare (*Lepus americanus*) populations show 9-11 year cycles in the northern boreal forest of North America (Keith *et al.* 1984; Krebs *et al.* 1986). However, other herbivores in these regions have also been observed to cycle, often in synchrony with the primary (voles, lemmings, or hares) species (e.g. Hörnfeldt 1978; Angelstam *et al.* 1984). The Alternative Prey Hypothesis (Lack 1954; Keith 1974) states that these cycles are caused by varying predation, and predicts that, as the preferred, or primary prey, decline in abundance from their cyclic peak, predators expand their diet to take alternative prey, depressing survival and numbers of these species. At the same time, reproduction and survival of predators are lowered. As primary prey begin to increase, predators start taking them again, releasing predation pressure on alternative prey and allowing these populations to increase. When primary prey are at their peak, predators take few alternative prey, allowing them to reach high numbers. A subsequent decrease in main prey then initiates another cycle.

The Alternative Prey Hypothesis has received much observational support in recent years, mainly from northern Fennoscandia (but also from the Taimyr peninsula in Siberia, see Summers and Underhill 1987). In northern Fennoscandia, voles show 3-4 year population cycles and serve as the primary prey for a variety of predators (Angelstam *et al.* 1984). As voles decline, dietary shifts by predators consistent with Alternative Prey Hypothesis predictions have been documented for red fox (*Vulpes vulpes*, Angelstam *et al.* 1984) and five species of owls (Korpimäki and Sulkava 1987; Korpimäki and Norrdahl 1989a; Korpimäki and Norrdahl 1991). Predation resulting in loss of muskrat (*Ondata zibethicus*) litters (Danell 1978), nest losses of black grouse (*Tetrao tetrix*, Angelstam *et al.* 1984), willow ptarmigan (*Lagopus lagopus*, Myrberget 1975; 1985 in Steen *et al.* 1988) and Oldsquaw ducks (*Clangula hyemalis*, Pehrsson 1986), and summer mortality of juvenile mountain hare (*Lepus timidus*, Angelstam *et al.* 1984), was all inversely related to cyclic vole numbers. In addition, heavy predation on passerine bird nests by mustelids during low vole densities was observed in Norway by Myrberget (1972, in Steen *et al.* 1988), and Jarvinén (1985); and Korpimäki and Norhdall (1989b) reported heavy predation on small mustelids by raptors during a decline of voles in Finland.

Observational or correlative evidence does not demonstrate, however, that predation is responsible for declines or cycles in alternative prey species (Krebs 1988). Many of the above studies in Fennoscandia only measured predation on alternative prey over one vole cycle (3-4 years), and conclusions may be relevant only to that particular cycle. Changes in survival of alternative prey may result directly (through starvation or exposure) or indirectly (through changes in behaviour) from inclement weather or poor food conditions. In addition, food and predation may interact, such that predation is higher when food for prey is at low levels (e.g. MacNamera and Houston 1987). For example, Steen (1978, in Steen *et al.* 1988) found the best years of willow ptarmigan chick production in Norway to coincide with the best years of grass production, while Marcström and Höglund (1980) showed that extremely bad weather with low temperatures and high precipitation can severely reduce willow ptarmigan recruitment in Swedish mountain areas. Herbivores that eat the same plants as the primary prey species may be affected by the poor condition of vegetation (due to overgrazing) during declines of primary species, forcing them to emigrate into new areas (Högstedt *et al.* 1991), or causing them to starve, suffer reduced breeding success, and become more vulnerable to predation (the Plant Cycle Hypothesis, Angelstam *et al.* 1985). In a review of the evidence for synchronous cycles of birds and mammals in Fennoscandia, Angelstam *et al.* (1985) could not reject the Plant Cycle Hypothesis, and concluded that predation is a necessary, but perhaps not sufficient, condition for the observed synchrony in the 3-4 year population cycles of small game and voles. Clearly, experimental manipulations of predation are needed to demonstrate whether predation can cause declines and synchronous cycles in primary and alternative prey species.

There is little experimental evidence for the Alternative Prey Hypothesis, and all of this work is from Fennoscandia. Marcström *et al.* (1988) removed most terrestrial predators from one of two islands in the north Baltic sea and reported higher brood sizes, a higher proportion of females breeding, and higher population sizes of adult capercaillie (*Tetrao umbellus*) and black grouse. When predators were present, tetraonid brood sizes and the proportion of females breeding successfully were each positively correlated with vole abundance. When predators were removed, neither of the above were correlated. Marcström *et al.* (1988) concluded that large vole populations resulted in large autumn grouse populations mainly because they reduced predation on breeding grouse. In an indirect test of the Alternative Prey Hypothesis, Lindström *et al.* (1987) provided additional food to predators during a cyclic decline in vole density and monitored survival of young grouse on that site and a control. The proportion of young grouse in autumn was higher on the experimental site than the control, and while the proportion decreased on the control relative to the previous year, it did not on the experimental site. Erlinge (1987) excluded mammalian and avian predators with fencing in southern Sweden and found higher survival of non-cyclic population of voles (*Microtus agrestis)* inside the exclosure. The seasonal spring decline of this population was less pronounced than in the control population. Although this experiment was performed in southern Sweden, where voles do not show multi-annual cycles (Erlinge *et al.* 1983), it demonstrates that predation may be a primary cause of the spring decline in vole populations. The above experiments suggest that predation pressure on alternative prey can increase during declines of preferred prey, and that changing predation pressure may play an important role in the ecology of alternative prey species.

In North America, there is evidence that the main predators of snowshoe hares follow a ten year cycle (e.g. Keith 1963; Nellis et al. 1972; Keith *et al.* 1977; Brand and Keith 1979) and take alternative prey when hare populations decline (Adamcik *et al.* 1978; Adamcik *et al.* 1979; McInvaille and Keith 1989). A few observational studies suggest that small herbivores sympatric with snowshoe hares may show ten year cycles roughly synchronous with those of the hares, but no experimental work has been done. Conspicuous ten year cycles of ruffed grouse (*Bonasa umbellus*) similar to that of the snowshoe hare have been noted by Keith (1963), however grouse peaks and declines tend to precede those of hares in northern regions, and to follow them in more southern areas such as Minnesota and Wisconsin (Keith and Rusch 1989). Erlien and Tester (1974) found a population of Franklin ground squirrels (*Spermophilus franklinii*) in northwestern Minnesota to show three distinct eleven year cycles over a 30 year period with peaks and declines occurring one year after those of snowshoe hares, but they were unable to determine the cause of the cycles. In central Alberta, Keith and Cary (1991) found a decline in the number of mustelids, sciurids, and porcupines caught incidentally in hare traps during the decline phase of one hare cycle, but again, these authors could not implicate predation as the cause of the declines. However, Gilbert and Krebs (1991) monitored red-backed vole (*Clethrionomys rutilus*) populations in the southwestern Yukon for 17 years and concluded these voles do not show 9-11 year cycles as originally thought (Gilbert *et al.* 1986), and that there is no simple interaction between the snowshoe hare cycle and *Clethrionomys* peaks. More studies, especially experimental manipulations of predation, need to be done to determine if predation can cause cyclic declines in alternative prey species in North America.

This thesis is, in part, an attempt to fill this need. Chapter 2 describes the results of an experimental exclusion of terrestrial predators on red squirrels (*Tamiasciurus hudsonicus*, Bangs) during a snowshoe hare decline in the southwestern Yukon. I monitored survival and density of red squirrels on a predator exclosure and an unmanipulated site to determine 1) if predation on red squirrels increased during a hare decline, and, 2) if so, whether or not this led to a decrease in density. Red squirrels are an abundant small herbivore occurring sympatrically with snowshoe hares in northern boreal Canada. There is some suggestion that red squirrels may serve as alternative prey for predators (Adamcik *et al.* 1978;1979), and that populations of red squirrels decline as hares decline (Keith and Cary 1991), but predation on red squirrels has not been examined.

My study was conducted in collaboration with the Kluane Boreal Forest Ecosystem Project, which is studying the dynamics of the snowshoe hare cycle and its effects on the boreal community. Information on hares, predators and small herbivores will be combined at a later date to give a more complete picture of predation during a snowshoe hare cycle.

For the purposes of this project, data on hare and predator densities from 1986 through 1992 are available in the appendices.

The abundance of food is thought to be the primary factor determining survival and population densities of red squirrels (C.Smith 1968; M.Smith 1968; Kemp and Keith 1970; Klenner and Krebs 1991). However, experiments with grey squirrels (*Sciurus carolinensis*) have shown that squirrels may adjust their behaviour according to perceived predation risk (Lima *et al.* 1985; Lima and Valone 1986), and that foraging behaviour may change with the abundance of food (Koprowski 1991). Thus, the availability of food may interact with predation to determine survival rates of red squirrels. To determine the ultimate cause for any changes in red squirrel survival or density during a hare decline, the effects of both food and predation on survival must be known. Chapter 3 describes experiments on the effects and interaction of food and predation on red squirrel survival. I supplemented food to individuals to determine 1) if the distribution and abundance of food affects adult survival, and 2) if supplemental food improves survival of adults over winter. I also monitored the survival of squirrels on four sites, a predator-exclosure, food addition, predator exclosure and food addition, and control site, in order to determine if food and predation have equal and/or additive effects on red squirrel survival. Despite recent conclusions that experiments should be designed to test interactions among various factors (Hilborn and Sterns 1982), this type of factorial experiment examining food and predation has only been conducted in one previous instance on voles (*Microtus ochnogaster*). Desy and Batzli (1989) found that protection from predators generally (but sporadically) improved adult survival, but that the availability of food had no effect on adult survival. Food and predation generally had additive and equal effects on vole density, but Desy *et al.* (1990) reported that these factors also interact, in that presence of predators reduced movement and inhibited the growth response to supplemental food.

NATURAL HISTORY OF THE POPULATION AND STUDY AREA

The study was conducted in the Shakwak valley (68° N, 138° W) near Kluane Lake, south west Yukon, Canada. The vegetation is dominated by white spruce (*Picea* *glauca*), interspersed with patches of aspen (*Populus tremuloides*) and clearings with willow (*Salix spp.*) and bog birch (*Betula glandulosa*) (Douglas 1974). White spruce produces a variable cone crop in August of each year, which constitutes the major food source for the red squirrel population in Kluane. As such, cone production of white spruce was measured on each of the study sites in August 1990 and 1991 (Appendix IV). Details concerning each of the specific sites used in this study are given in each chapter. The Shakwak valley and relative locations of the study sites are shown in Figure 1.1.

The climate in Kluane is considered semi-arid, with long dry winters and short cool summers. Mean monthly temperatures were generally colder than the 30 year averages in the winter of 1990-91, and generally warmer than the averages in 1991-92. Data and analysis of weather conditions during the study are provided in Chapter 2.

Red squirrels maintain individual territories varying in size from 0.25 ha to 1 ha (C.Smith 1968), depending on the available food supply and habitat (Klenner 1991). In Kluane, territories average 0.3 ha for males and 0.44 ha for females (Price *et al.* 1986). Territories can vary considerably in quality and their ability to sustain a squirrel over winter (C.Smith 1968; Kemp and Keith 1970; Gurnell 1983). Marginal territories are occupied mainly by juveniles and often abandoned, while high quality territories are usually occupied by adults and defended year round (Rusch and Reeder 1978). Adult red squirrels are very sedentary, rarely moving from their territory (Chapter 2). Each territory, with the exception of some marginal ones, contains one or more cone caches, or middens, considered essential for overwinter survival (Kemp and Keith 1970). Middens are traditional and may serve generations of squirrels, and thus are composed of many thousands of old cone bracts (discarded after eating the seeds), into which tunnels, storage chambers for cones, and sometimes nests, are dug. Middens are very conspicuous, and tend to be the activity centre of each territory.

The mating season is variable in Kluane, with adult males becoming scrotal (able to breed) as early as late December, although most mating occurred in March during this study. Most females produced only one litter per year in this study, although in 1992 five females produced a second litter after the death of their first (Chapter 2). Female red squirrels commonly produce two litters in eastern Canada, but generally only one in western Canada (Lair 1985). Litter sizes ranged from 1-6 during the study. Neonates are born helpless after a gestation period of 36-39 days, and remain in the nest (in a tree, hollow log, or underground) until 50 days of age. Weaning occurs at roughly 70 days of age. Some females 'bequeath' all or part of their territory to one of their offspring (Price 1989), while other offspring are aggressively forced off to find their own territory. Juveniles may make exploratory movements up to several kilometres away (Larsen 1992), but frequently settle near their natal territory (Stuart-Smith, unpubl. data).

Red squirrels probably live between five and ten years (Gurnell 1984), with mortality thought to be highest during the first year. Estimates of annual juvenile mortality range from 0 to 70 % (Kemp and Keith 1970; Rusch and Reeder 1978), and from 10-85% in Kluane (Chapter 2; Boutin, unpubl. data). Adult mortality has been reported between 40 and 90 % annually, with high seasonal, geographic, and yearly variation (Kemp and Keith 1970; Rusch and Reeder 1978). Predation is generally not assumed to be a major determinant of mortality rates (Gurnell 1984), but there have been no published studies of predation on red squirrels.

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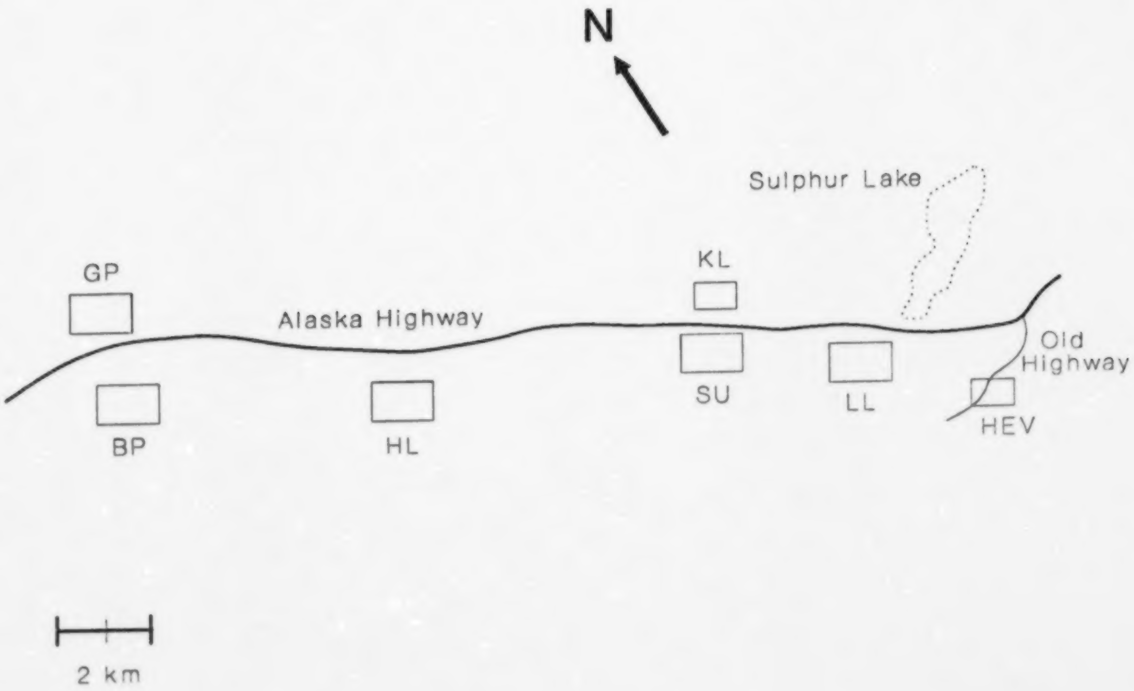
N
Sulphur Lake
GP
KL
Alaska Highway
Old
Highway
BP
HL
SU
LL
HEV
2 km

Figure 1.1. Location of the study sites relative to each other. GP=Gravel Pit, BP=Beaver Pond, HL=Hungry Lake, SU=Sulphur, KL=Kloo, LL=Lloyd, HEV=Heaven.

CHAPTER 2

PREDATION ON RED SQUIRRELS DURING A SNOWSHOE HARE DECLINE

INTRODUCTION

The red squirrel (*Tamiasciurus hudsonicus*) is an abundant small herbivore occurring over much of the boreal forest in North America. Its density is thought to be determined primarily by the abundance of food (C.Smith 1968; Gurnell 1983; Sullivan 1990; Klenner 1991), which in boreal regions, consists mainly of conifer seeds. Many conifers produce irregular mast crops, and populations of squirrels have been observed to fluctuate with the size of the cone crop (C.Smith 1968; M.Smith 1968; Kemp & Keith 1970), although densities may also be reduced by inclement weather (Nixon & McClain 1969). The impact of predation on red squirrel survival rates is not well known, but predation is generally not considered to be an important factor in determining red squirrel densities (Gurnell 1987). However, predation on red squirrels has not been examined.

Species that exhibit cycles such as voles, lemmings, and snowshoe hares (*Lepus americanus*) are characteristic of northern vertebrate communities (Taitt & Krebs 1985; Krebs *et al.* 1986), and may influence the abundance of other prey species in their community by affecting predation pressure from shared predators. When the most abundant prey or preferred prey declines, predators may begin taking alternative prey, depressing survival and numbers of these species (Lack 1954; Keith 1974). Many species of small herbivores have been observed to decline simultaneously with, or shortly after, the primary prey species in their community, and to exhibit cycles of the same period as the primary prey species (e.g. Danell 1978; Hörnfeldt 1978; Angelstam, Lindström & Widén 1984; Summers & Underhill 1987; Steen *et al.* 1988; Keith & Cary 1991). Snowshoe hares in North America undergo nine to eleven year cycles (Keith 1963; Keith *et al.* 1984; Krebs *et al.* 1986). Lynx (*Lynx canadensis*), coyote (*Canis latrans*), great horned owl (*Bubo virginianus*), and northern goshawk (*Accipiter gentilis*), are the main predators of snowshoe hares, and are known to eat red squirrels also (Rusch & Reeder 1978). If red squirrels serve as alternative prey for these predators, then squirrel densities may be expected to decline with or shortly after hare densities.

In central Alberta, where hares and red squirrels occur sympatrically, Keith & Cary (1991) showed that numbers of red squirrels caught incidentally in hare traps decreased as hares declined. However, Keith & Cary (1991) did not determine whether this decline was due to predation. The production of tree seeds was not monitored, and the decline in squirrel numbers may have been due all, or in part, to seed crop failures coinciding with the hare decline. In addition, trapping effort was not kept constant, as the number of traps available to catch red squirrels varied with the number of hares caught, making conclusions tenuous. Rusch & Reeder (1978) and Kemp & Keith (1970) studied red squirrels in the same area during a cyclic increase of snowshoe hares. Although densities of alternative prey may not necessarily be expected to increase with those of primary prey, studies in Fennoscandia (e.g. Angelstam, Lindström & Widén 1984) have found this to be the case for some species of alternative prey (e.g. Black grouse (*Tetrao tetrix*) and Mountain hare (*Lepus timidus*)). Rusch & Reeder (1978) found little variation in spring population densities over their four year study and concluded that red squirrels maintain constant population densities despite the fluctuations of hares, predators, and mast crops in central Alberta. Kemp & Keith (1970) also found little variation in adult numbers, but showed red squirrel fur returns in Alberta (over 34 years) to be significantly correlated with spruce cone crops, and concluded that squirrel populations fluctuate with the size of the cone crop. However, neither of the above studies measured predation of red squirrels, and changes in predation rates during the hare cycle may not have been detected.

The objectives of this study were to determine (1) if predation on red squirrels increased during a snowshoe hare decline, and, (2) if so, whether or not this led to a decrease in red squirrel density. I compared survival of squirrels during a hare decline on a site where mammalian predators were excluded with that on an unmanipulated site. I predicted that predation on squirrels would be lower on the site where potential predators were excluded than on the control, and that predation on squirrels would increase as hare densities decreased. I monitored food levels and weather conditions during the study and attempted to determine the proximate cause of mortality for individuals. Adult and juvenile survival was monitored separately, as the survival of juveniles may be lower than that of adults (Rusch & Reeder 1978), and may affect population density to a different degree than adult survival. The study was conducted in conjunction with the Kluane Boreal Forest

Ecosystem Project, as part of an ongoing study of the snowshoe hare cycle and dynamics of the boreal forest community.

METHODS

Study Area and Background

The study was conducted in the Shakwak valley near Kluane Lake (61° N, 138° W) in the southwest Yukon Territory, Canada. The vegetation is dominated by white spruce (*Picea glauca*), with a patchy understory composed primarily of willow (*Salix spp.*) and bog birch (*Betula glandulosa*) (Douglas 1974).

Snowshoe hare populations in the Kluane region reached peak densities in 1989 and 1990, began to decline during the winter of 1990-91, and had fallen to 8 % of peak densities by October 1992 (Appendix I). The greatest mortality occurred during winter 1991-92, where populations declined from 80 % to 18 % of peak densities. Indices of coyote and lynx numbers (determined from track counts) were high in winter 1990-91 and peaked in winter 1991-92 (Appendix II). The number of breeding pairs of resident Northern Goshawks peaked in 1990 and declined in 1991 and 1992, while numbers of migratory Harlan's Hawk (*Buteo harlanii*) pairs remained relatively stable from 1990 to 1992 (Appendix II). The number of Great Horned Owl pairs increased from 1990 to 1991, and peaked in 1992 (Appendix II). However, breeding success of goshawks and great horned owls was highest in 1990 and 1991, and completely failed in 1992. Harlan's Hawks experienced similar breeding success in 1990 and 1991, with only slightly lower success in 1992 (Appendix II). The two years of my red squirrel study, 1991 and 1992, thus coincided with a substantial decline in the hare population and with high or peak densities of most predators.

Potential alternative prey species for predators in the Kluane region, besides red squirrels, include voles (*Clethrionomys rutilus Microtus pennsylvanicus*), mice (*Peromyscus maniculatus*), chipmunks (*Tamias minimus*), spruce grouse (*Canachites canadensis*), ruffed grouse (*Bonasa umbellus*), willow ptarmigan (*Lagopus*), and arctic ground squirrels (*Spermophilus paryii*). Red squirrels represent the highest biomass of any of these species in the Shakwak valley (Appendix III).

Cone production of white spruce (number of trees producing cones and average number of cones produced per tree) on the sites used in this study was significantly higher in August 1990 and 1992, when it was moderately heavy, than in August 1991, when there was a virtual cone failure (Appendix IV). Red squirrels in Kluane depend heavily on seeds from white spruce cones for food, particularly in winter.

Mean monthly temperatures during the study were obtained from the weather station in Burwash Landing, Yukon, 40 km from the study area (60 km by road).

Trapping of Squirrels

Squirrels were monitored on a mammalian predator exclosure (Beaver Pond) and a control site (Sulphur). The exclosure was set up in 1986 by the Kluane Boreal Ecosystem Project, and consisted of a one km^2 area enclosed by an electric fence two m high which effectively excluded lynx and coyotes, but did not prevent squirrel movement. Squirrels were studied on a 40 ha site within the exclosure, comparable to the 40 ha control site. Both sites had similar vegetation, although spruce on the exclosure (average diameter breast height 23.5 ±15.5, n=86) were generally older and thus larger than spruce on the control (average d.b.h. 14.7 ±11.2, n=86, two-tailed *t* test= 5.27, df=170, P=.001), and there were more open meadow patches on the exclosure than on the control. The location of the sites relative to one another is shown in Figure 1.1. (Chapter 1).

Squirrels were trapped at middens with live traps (Tomahawk 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter. Each squirrel was marked with two numbered metal ear tags (Monel no.1) with short pieces of coloured plastic coated wire or coloured plastic disks (one cm diameter) threaded over them such that each individual had a unique colour combination and could be identified from a distance. Animals were weighed with a Pesola scale and sex, age class (adult or juvenile/young of the year), coat condition (1 = very ragged, patches of fur missing, through 5 = excellent, shiny, no fur missing), and reproductive condition (males: scrotal, nonscrotal; females: non-breeding, pregnant, lactating) recorded. Pregnant females were recognizable by their extended bellies and relatively high weights, and lactating females by their pink and swollen nipples through which milk excretion could be stimulated. Traps were set at middens and opened for one-two hour sessions until the resident squirrel was caught (which usually required one to three trapping sessions) at least once in November 1991, March and April 1991 and 1992, and at least every 10 days from May through August 1991 and 1992.

Adult Survival

Each adult squirrel was confirmed alive or dead once per week from March through August 1991 and 1992 through trapping, observation or radio-location. At least half the adults on each site were radio-collared with small (4 g) radios (Hollohil Systems Ltd., Woodlawn, Ontario, Canada) in 1992. Transmitter signals were monitored with hand held receivers (Telonics) and directional antennae once per week, during periods when squirrels were most likely to be active (10 am-3 pm winter, 6-11 am and 7-10 pm summer), and classified as active or inactive depending on the presence of changes in signal amplitude. Squirrels classified as inactive (those with signals of constant amplitude) were located visually to determine if they were dead. Radios had a range of 1-5 km and a battery life of six months. The Kaplan-Meier survival estimator (Pollock *et al.* 1989) was used to calculate survivorship curves for adults on the control and the exclosure each year. The Kaplan-Meier method allows for the entry of animals into the study at any time, (i.e. so sample size can be kept high despite high death rates) and makes no assumptions about the shape of the survival curve. It also accounts for individuals with radio-collars that failed and for individuals without radio-collars whose fate is unknown (censored animals). Survivorship curves were compared between sites within years, and between years within sites, with a log-rank (LR) test (Pollock *et al.* 1989), which calculates an approximate Chi-square statistic with one degree of freedom based on a series of 2 x 2 contingency tables.

The fates of radio-collared squirrels that died were ascertained from the remains found with the radio. All dead squirrels were apparently depredated or scavenged, i.e. no dead squirrel was found complete (see results). Where only the tail and/or the stomach remained, the cause of death was classified as mammalian predation (K.Larsen, pers. comm.), and where a circle of fur tufts and sometimes bits of the skull or tip of the tail remained, cause of death was classified as avian predation (Gurnell 1987). Where insufficient evidence remained to determine cause of death, it was classified as unknown. Squirrels without radio-collars that disappeared from their territory for more than 3 weeks were presumed dead, due to the very low dispersal rates of adults (see Results).

All squirrels on each site were enumerated by trapping at middens in March, May, and August of each year, as well as in November 1991. As red squirrels are territorial and very sedentary (see above), a complete enumeration of every resident individual on each site was possible. Adult survival from September through mid-November 1991 and from December 1991 through February 1992 was determined by comparing the percentage of squirrels surviving through each time period. All G tests had one degree of freedom, unless otherwise stated.

Characteristics of Depredated Squirrels

Predation on squirrels could vary between years if the physical condition of squirrels varied between years due to extrinsic factors such as weather and size of the cone crop. I compared the average body weights of adults in March by sex within sites between years, and between sites within years, with mixed-factor ANOVAs (year as a random factor). To determine if squirrels taken by predators were in poorer condition than those surviving, I compared the March weights of surviving and depredated adult individuals. Body weights may be confounded by seasonal and asynchronous reproductive changes so I analyzed weights by sex and used only weights collected in early March before the breeding season began.

I also examined the weights of depredated female adults for a change in weight in the two weeks prior to predation. A high weight loss may indicate disease or starvation (or parturition, which may be confirmed through lactation).

Juvenile Survival

Juvenile squirrels were monitored from birth. Pregnant females (identified through weight gain and change in nipples from small to large and dark) were trapped every three days for evidence of parturition, as indicated by a drop in weight and the start of lactation. Once parturition had occurred the nest containing the young was located (through observation or radio-location of the mother at night or on hot afternoons) and the number and sex of young recorded. Neonates were too small (10 g) to eartag; I returned to the nest 4 weeks after birth when the young were approximately 50 g, and fitted them with numbered and coloured eartags as for adults. In 1992 I also clipped the fur between the shoulderblades and attached small radios (3 g, Biotrack, Wareham, Dorset, England) with cyanoacrylate glue to 28 of the 41 young on the control and 18 of the 27 young on the exclosure that reached five weeks of age. These radios had a range of 150-300 m and a battery life of six weeks, and were coated with cayenne pepper and epoxy to prevent the mother from chewing on them. Glue-on radios did not appear to affect the juveniles; when the radio fell off the skin underneath was pink and healthy and the fur grew back shortly afterwards. Glue-on radios often fell off after two weeks, by which time the young had usually emerged. Young were located and trapped before or shortly after this to remove the radio and outfit them with a radio-collar as for adults. In 1991 I radio-collared over half of all emergent juveniles on both sites; in 1992 all but three of the juveniles known to emerge on the control, and all but one of the juveniles seen emerged on the exclosure were fitted with radio-collars. In 1991 each juvenile with a radio-collar was monitored every four days, and in 1992 we attempted to monitor each one every day. Survivorship curves were calculated for juveniles after emergence with the Kaplan-Meier method each year for the control and the exclosure. Curves were compared between areas and years with the log rank test. I did not combine radioed and non-radioed juveniles for the survivorship analysis because I did not closely follow uncollared juveniles after their emergence and so could not accurately determine their fate or timing of death. I compared the percent survival of all juveniles (with and without radios) from birth to emergence and to mid-September between sites within years, and within years between sites, with G-tests. A juvenile was considered an adult once it reached March of the year following its birth.

Predator Sightings and Scavenging

All predators seen on the sites were recorded, and the total number of predator sightings per 100 hours was calculated for each site, each year.

Predation could be overestimated if predators scavenged squirrels that died from other causes (Boutin *et al.* 1985). In order to determine how much scavenging was occurring I randomly placed dead squirrels (road kills or trap deaths) on each site in July of each year. Four squirrels were placed out on each site in 1991, and eight on each in 1992. Squirrels were placed on the ground in similar locations each year. Small spools of thread were taped to the base of squirrels' tails and one end of thread tied to the base of a tree or bush so that the carcass could be retrieved if cached by a scavenger and some clue as to the identity of the scavenger determined. Carcasses were checked daily for ten days and any marks or removals noted.

RESULTS

Weather

Mean monthly temperatures in 1992 tended to be several degrees warmer than those in 1991 (Figure 2.1), particularly November (8° warmer), January (7° warmer), and March (4° warmer). April and May 1992, however, were colder by two and three degrees respectively than these months were in 1991. Mean monthly temperatures in 1991 were similar to the 30 year averages for each month, except for November (9.5° colder) and January (3° colder). In 1992, mean monthly temperatures were slightly warmer than the 30 year average for each month, especially December (3° warmer) March (4°warmer), except for April (4° colder) and May (1.5° colder). In 1991, snow cover disappeared on April 30, but in 1992 snow remained on the ground until May 20.

Adult Survival

In 1991 I monitored the survival of 84 adults on the control and 51 adults on the exclosure. In 1992 I monitored 94 adults on the control and 51 adults on the exclosure. Eighteen of these on each site were radio-collared from January through March, and a total of 35 on the control and 24 on the exclosure were radio-collared from March through August. Adults were extremely sedentary; of 59 adults with radio-collars, only 5 moved permanently from one territory to another, with only one of these moving off the study area. The average distance moved was 44 ± 19 (s.d.) m, with a maximum of 67 m. Adults without radio-collars that disappeared from their territories were searched for during at least two, three hour periods when squirrels were likely to be active, in a circle of 100 m radius around their midden (if considered approximately circular, territories in Kluane have an average radius of 30 m, Price *et al*, 1986). None were found. Therefore, disappearance was attributed to death, and collared and uncollared animals were combined for survivorship analysis. There was no difference in survival of collared and uncollared animals (1992, G =0.520, P =0.471).

None of the adult squirrels with radio-collars were found dead of something other than predation. On the control, 50% of the known kills were avian and 21 % were mammalian; on the exclosure all known kills were avian (Table 2.1). On each site there were three kills classified as unknown. These were cases where no remains of the squirrel was found, but the plastic tubing serving as the collar for the radio was filled with blood. It is likely that these individuals were depredated by great horned owls, which remove the head of their prey before eating the entire animal (C. Rohner, pers. comm.). There were four radios on the control known to be working well that abruptly ceased to transmit signals, concurrent with their owner's disappearance. Considering the low probability of adult dispersal and the fact that no such cases occurred on the predator exclosure, these were likely depredations by lynx or coyote in which the radio was destroyed. Adding these four cases to the mammalian total produces an equal impact of avian and mammalian predators on adults. As all radio-collared squirrels were depredated, all adults without radio-collars that disappeared were assumed depredated.

There was no difference in adult survivorship between the control (.81 ±.04) and the predator exclosure (.73 ±.06) from March through August 1991 (LR =1.58, P >.4, Table 2.2). During this period 16 of 84 (19 %) squirrels died on the control, while 12 of 51 (24 %) died on the exclosure (G = 0.38, P =0.538). Upper and lower bounds representing maximum and minimum survivorship were calculated by assuming all censored animals (those who disappeared or whose collars failed) to be alive or dead respectively (Table 2.2).

Adult survival from September through November 1991 was high and did not differ between the two sites (97.1 % control, n = 68; 97.6 % exclosure, n=42). There was also no difference in survival from December through February 1992 (98.5 % control, n=66; 100 % exclosure, n=41). None of the 36 adults with radio-collars were depredated on either site in January or February 1992.

There was, however, a significant difference in survival between the sites from

March through August 1992 (LR = 4.56, P <.05) (Table 2.2, Figure 2.2). Thirty-six of 94 adults (38 %) on the control were depredated, while only 10 of 51 (20 %) on the exclosure were depredated (G = 5.19, P=0.023). Survivorship on the control decreased significantly from 1991 to 1992 (LR = 6.66, P <.01), but there was no change in survivorship on the exclosure from 1991 to 1992 (LR = 0.35, P >.4)(Table 2.2).

Characteristics of Depredated Squirrels

Male and female adults were taken by predators in equal numbers in both years, on both sites. The sex ratio in the population did not deviate from 1:1 in either year. However, in both 1991 and 1992 on the control, but not on the exclosure, there was a strong seasonal pattern of survival. Virtually all males that died did so in March, April or May, while most females that died did so in May, June, July and August (Figure 2.3).

I used a mixed factor (year as random) two-way ANOVA to determine if the weights of adults (both surviving and depredated) differed between sites or years. Sexes were analyzed separately. There was no difference in March body weights of male adults between the sites (F=0.01, df=1,67, P=.93), but there was a strong year effect (F= 7.99, df=1,67, P=.006), with males on both sites showing higher March weights in 1992 than in 1991 (Table 2.3). The two-way ANOVA for females produced a significant interaction of treatment and year (F=4.29, df=1,93, P=.041), caused by weights of females on the exclosure being higher in 1992 than in 1991, whereas weights of females on the control were similar in 1992 and 1991.

A mixed factor (year as random) three-way ANOVA was used to analyze differences in weight between depredated and surviving individuals (sexes analyzed separately) (Table 2.3). For males, there was a significant three-way interaction between year, treatment, and survival class (F=4.16, df= 1,63, P=.045). This was produced by depredated males weighing more than surviving males on the exclosure in 1992, while the reverse was seen on the control in 1992 and on both sites in 1991. There was no difference in the weights of depredated and surviving males for any of the four treatment-year combinations (Tukey HSD tests, all P's >.05). Extremely small sample sizes on the exclosure in 1991 make conclusions tenuous, however. When males on the control were analyzed with a separate two-way ANOVA, the mean weights of depredated males were significantly lower than those of surviving males (F=25.04, df=1,39, P=.039). On the exclosure, there was no difference in the weights of surviving and depredated males in either year (F=2.48, df=1,24, P=.124).

For females, the three-way ANOVA produced a significant interaction of year and survival class (F=4.89, df=1,93, P=.029), and year and treatment (F=6.20, df=1,93, P=.0145). Tukey tests did not reveal any significant differences among the means (all P's >.05), but in 1991 the weights of females that died were slightly higher than the weights of females that survived, whereas in 1992 they were similar (Table 2.3). A two-way ANOVA confirmed that, in 1991 on both sites, females that died had higher body weights than those that survived (F=6.81, df=1,43, P=.013). The year-treatment interaction is essentially the same as that discussed above, where, in 1992, females on the exclosure had higher weights than females on the control. A two-way ANOVA for 1992 showed this to be the case (F=4.63, df=1,37, P=.036). In all cases weights of females that died were never lower than those of females that lived. However, as for males, small samples sizes for depredated females prevent strong conclusions from this and the above analysis.

As most females died in summer (Figure 2.3), March body weights may not reflect their condition when depredated. Thus, I examined changes in body weight in the two weeks prior to depredation. There was no consistent trend in weight change; 6 females lost an average of 23.5 g, 6 gained an average of 15.8 g, and 5 remained unchanged. The maximum amount of weight lost was 29 g, which was a high, but not unusual, weight loss over lactation (mean weight loss was 11.8 + 20.0 g (s.d.), n=28; range from 65 g lost to 22 g gained). None of the females had a lower weight just prior to predation than she did in March. Of the 21 females depredated on the control in 1992, 10 (48%) were lactating when depredated, 3 (14%) were pregnant, and 8 (38%) were non-breeders or had recently stopped lactating. I could not examine weight loss prior to predation for males as most males died in March and April when I did not trap every week.

Juvenile Survival

Pre-emergence

In 1991, survival of juveniles before emergence (up to 50 days of age) was high on both the control (92 %) and the exclosure (74 %) (Table 2.4). Lower survival on the exclosure (G= 4.128, P=0.042) was due entirely to the complete loss of two litters (six offspring) when their mothers were depredated a week after their birth. All mothers on the control survived until their litters were at least 50 days old. Young did not carry radios prior to 50 days in 1991, thus the cause of death of the young on the control could not be established.

Survival of juveniles in the nest was significantly lower in 1992 than in 1991 on the control (27 % vs 92 %, G =73.35, P <.001), but not on the exclosure (71 % vs 74 %, G =0.050,P >.8) (Table 2.4). High mortality among juveniles born on the control in 1992 was due primarily to pre-tagging loss; most of the young (64 %) died before reaching 35 days of age. Nineteen of 32 first litters failed completely, and 53 % of the other 13 litters lost one or more juveniles before emergence. Five of the 19 females that lost their litter produced a second litter, which experienced higher survival in the nest. As radios could not be glued onto the young until they reached 35 days of age, I was not able to determine exact cause of death of the neonates. However, 28 of the 41 young that reached 35 days in 1992 had glue-on radios, and three of these died of apparent starvation (Table 2.5), as they were found dead in their nest or hanging from branches, with no visible marks or blood present. Two of the seven confirmed deaths on the exclosure also appeared to be from starvation. Young that reached 35 days were sluggish and slow to develop for their age (Boutin, unpubl.).

Post-emergence

Survival of juveniles radio-collared after emergence was similar on each site in both years (Table 2.2). In 1991, seven of the 28 (25 %) radio-collared juveniles on the control and five of twelve (42 %) on the exclosure were depredated (Table 2.5) (G = 1.07, P =0.301). In 1992, six of the 32 (19 %) radioed juveniles on the control were depredated, while five of 21 (24 %) radioed juveniles were depredated on the exclosure (G =0.19, P=0.663). Juveniles with radios that failed were likely dead. Juveniles displayed slightly higher dispersal than did adults, but distances moved were short. In total (1991 plus 1992), 13 of 77 (17 %) radio-collared juveniles dispersed from their natal territories, with an average distance moved of 50 ± 31 (s.d.) m, and a maximum of 115 m. Only three of these individuals moved to where they would not have been found through regular trapping and observation.

Juveniles displayed significantly lower survival from June (post-emergence) through August than did adults over these months, in both 1991 and 1992, on both sites. In 1991 on the control, 51 % of juveniles survived while 91 % of adults did ($G = 27.48$, $P < .001$); on the exclosure 50 % of juveniles survived and 87 % of adults did ($G = 6.68$, $P = 0.01$). In 1992, 58 % of juveniles and 81 % of adults survived on the control ($G = 10.12$, $P < .001$); on the exclosure 64 % of juveniles and 86 % of adults survived ($G = 5.41$, $P = 0.020$).

Survival of males and female juveniles was generally similar in both years, both in the nest and after emergence, except on the control in 1992 where there was a trend toward higher female survival after emergence (7 of 19 males and 12 of 18 females survived, $G = 3.35$, $P = 0.067$). The sex ratio of juveniles produced did not differ significantly from 1 : 1 in either year, on either site.

Population Densities

On the control, population density (adults and juveniles) was lower in August of 1992 than in August of 1991 by 16 % (Figure 2.4). Density in March 1992 was higher than in March 1991, although densities in May were similar in both years.

On the exclosure, density was higher in August 1992 than in August 1991 by 19 %. Densities in both March and May were higher in 1992 than in 1991 (Figure 2.4).

Predator Sightings and Scavenging

In 1991, a total of 722 hours were spent on the control and 453 hours on the exclosure. In 1992, 1267 hours were spent on the control and 346 on the exclosure. The discrepancy is due to the higher number of people that worked full-time on the each site; two in 1991 and three in 1992 on the control, vs one in both years on the exclosure. Fewer predators were seen in 1992 than in 1991 (Figure 2.5). In 1991, considerably more predators were seen on the control than on the exclosure, but in 1992 there was little difference between the sites (Figure 2.5). In 1991, there were 76 avian and 6 mammalian predator (all coyotes) sightings on the control and 31 avian and 1 mammalian (a lynx that got into the exclosure for a week) on the exclosure. Most avian predator sightings (47 of 81) were of goshawks. In 1992, 32 avian and 1 mammalian predators were spotted on the control, and only 12 avian and 1 mammalian (a weasel) seen on the exclosure. Harlan's hawks were the most common avian predator seen (20 of 44 sightings).

It is unlikely that squirrels considered to have been depredated actually died of starvation and were subsequently scavenged before I could locate the carcass. I located the majority (19 of 25) of squirrel depredations within two days. No carcass placed on the exclosure was scavenged in either year, while in 1991 one of the four carcasses placed on the control was removed on the eighth day after placement (probably by a coyote or lynx as only the tail remained and no tufts of fur were found). In 1992 five of the eight dead squirrels on the control were taken, on the second, forth, fifth, sixth and eighth days. Carcasses were removed from the sites and completely eaten. As no carcasses were removed on the exclosure, scavenging on the control was probably done by mammalian predators.

DISCUSSION

This study is the first, to my knowledge, to demonstrate experimentally that predation on an alternative prey species can increase as snowshoe hares decline. Several authors have found trends in numbers of sciurids, tetraonids, and mustelids indicating these species decline shortly before (Keith & Rusch 1989) or after hares (Erlien & Tester 1984; Keith & Cary 1991). In addition, there is some evidence from analysis of coyote, lynx, great horned owl, and red-tailed hawk diets that these predators take alternative prey as hares decline (Keith *et al.* 1977; Adamcik,Todd & Keith 1978; Adamcik,Todd & Keith 1979), but there is no experimental evidence which clearly demonstrates that predation, and not other factors such as food availability or weather conditions, is responsible for the observed declines in alternative prey species. The need for experimental manipulation was demonstrated in this study, which could have been confounded by the white spruce cone failure in 1991 and colder than normal temperatures in spring 1992. Had I not manipulated predation and monitored radio-collared individuals to determine cause of death, I would not have been able show that predation, and not low food abundance or inclement weather, was the proximate cause of lower adult survival in 1992.

I cannot rule out, however, that the lack of spruce cones or cold temperatures affected the physical condition and behaviour of the squirrels in 1992, predisposing them to predation. McNamara & Houston (1987) argue that starvation and predation can interact strongly, such that animals may increase their risk of predation in order to avoid starvation, and that it is difficult to determine the importance of food from observations on the rates at which animals die from starvation. However, there are two lines of evidence suggesting that higher predation was not solely the result of low food abundance.

First, survival on the control was virtually one hundred percent from September 1991 through March 1992, and the weights of adults on both sites were generally higher in March 1992 than in March 1991. This suggests that food levels were not insufficient, despite the cone failure in 1991. Squirrels were observed clipping shoots and eating the buds of spruce in great numbers in March, April and May 1992. White spruce cones are initiated 18 months before maturation, and the cone buds differentiate the summer preceding the crop (Owens & Molder 1981). As the cone crop in 1992 was heavy, immature cone buds would have been present in high numbers in early 1992, offering a protein rich food source (Kramer & Kozlowski 1960, in Kemp & Keith 1970). Kemp & Keith (1970) and C.Smith (1968) observed higher overwinter survival and increased rates of reproduction in red squirrels immediately before a medium-to-heavy cone crop, which Kemp & Keith (1970) attributed to the presence of large numbers of spruce buds. In addition to buds, squirrels may have utilized fungi. Mushroom production was substantial in summer 1991 (pers. obs.), and squirrels were seen caching these in trees in great numbers. The fruiting bodies of fungi show high levels of essential nutrients with a crude protein content similar to that of spruce seeds (Grönwell & Pehrson 1984), and fungi may have composed a critical part of the winter diet. Maser, Trappe & Nussbaum (1978) found the stomachs of red squirrels in coniferous forests in Oregon to contain primarily fungi in summer. Thus, despite the cone failure, food may not have been limiting in 1992.

Second, if squirrels were at risk of starvation, I would expect to see evidence of poor condition in at least some individuals, and that depredated individuals would be in poorer condition than those that were not depredated. Yet, as mentioned, body weights in March 1992 were generally higher than in March 1991, and there was no evidence of poor condition (either in coat condition or flea load) in the general population. S.Boutin (pers. comm.) found that squirrels had very ragged coats and numerous fleas the year following a complete cone failure, suggesting that coat condition and flea load are a reasonable measure of energetic stress. In addition, there was no clear indication that depredated individuals were in worse physical condition than surviving individuals. It is possible, however, that my measurements were too crude to detect substandard individuals, as depredated individuals may have had internal parasites or other invisible weakening conditions. Temple (1987) found that grey squirrels (*Sciurus carolinensis*) taken by a red-tailed hawk (*Buteo jamaicensis*) were substandard in ten of the 14 categories he used to quantify condition, including body weight, loin fat mass, and prevalence of endo and ectoparasites.

One criticism of this study is that it had no replication, and that it only demonstrated a difference between two areas and not a true effect. However, the conclusion is supported in that survival and density of red squirrels on several other unmanipulated sites in the same study area was also lower in 1992 than in 1991 (S.Boutin, unpubl. data). It is unlikely that higher predation on the control was due to its being a 'hotspot' for predators. In 1992, predator sightings were higher on the exclosure than the control, and there were two great horned owl nests within the predator exclosure, while the nearest known avian predator nest to the control was 2 km away (F.Doyle, pers. comm.). In addition, if there was some factor or factors operating on the control and not on the exclosure that predisposed squirrels to predation, squirrels on the control may be expected to show evidence of poor condition. For example, Rusch & Reeder (1978) found squirrels residing in aspen forest, considered inferior habitat, to have significantly lower body weights and survival than those living in spruce. As discussed, I found no difference in body weights of squirrels between the two sites. If anything, conditions on the control appeared overall to be more favourable for the squirrel population, as there was a slightly, but not significantly higher, density, percentage of females breeding (59 vs 45 %, 1991; 75 vs 67 %, 1992), and average litter size there (2.6 vs 2.3 1991; 3.34 vs 3.21 1992). The control was situated on a slight south facing slope and at a lower elevation than the exclosure, which sloped north and was exposed to high winds. Thus, if anything, squirrels on the control would be expected to show higher, and not lower, survival. The higher density on the control was not likely a factor causing the higher predation observed there. Density on the control was similar in both 1991 and 1992, while predation there was twice as high in 1992, implying that predation on red squirrels is not density dependent (at least over the densities observed).

Only the poor survival of neonates on the control in 1992 suggests that conditions there may have been adverse in spring 1992. The neonates almost certainly died of starvation or exposure rather than predation. Weasels, due to their small size, are virtually the only predator able to gain access to red squirrel nests in Kluane, and no weasels or weasel tracks were sighted on the control in 1992. As well, weasels probably kill all the neonates in the nest (see Jarvinén 1985), and there were many litters in which only one or two neonates died. Young that survived grew slowly and seemed sluggish for their age (Boutin, unpubl. data), suggesting that malnutrition was occurring. Young on the exclosure were also slow to develop, but fewer neonates died there. However, monitoring of pregnant females on the exclosure was not as frequent as that on the control, and I may have missed some females that had litters and lost them soon after birth, which would increase (artificially) my estimate of neonate survival on the exclosure relative to the control.

The distinct seasonal patterns of survival seen in the adult sexes probably relate to the breeding season; in Kluane males become scrotal (able to breed) in late winter and remain so through early June, while females generally give birth to their young late April through May and lactate through July. Most mating activity occurs in March and April (pers. obs.), coinciding with the period of highest male mortality. Behavioral oestrus lasts one day at most in red squirrels (Lair 1985), and males have been observed to travel extensively during the mating period (Rusch & Reeder 1978), presumably seeking out females to mate with. Males may be more vulnerable to terrestrial predators while seeking mating opportunities, which would account for the high mortality of males in early spring, and for the lack of such a pattern on the predator exclosure. Females, however, may be more vulnerable to predation when lactating. The high energy cost imposed by lactation (Havera 1979) may cause them to lose condition (and thus be more vulnerable to predation), or force them to spent greater amounts of time foraging (increasing their risk of predation). In June and July of both years, I observed females foraging until midnight, whereas males usually went into their nests around ten at night. Foraging at dusk may increase the risk of predation by nocturnal predators such as great horned owls. Rusch and Reeder (1978) found a similar seasonal pattern or mortality; heavy mortality of adult females occurred from July through September (parturition to weaning), while the highest mortality of males occurred during the breeding season (March-June).

The population density of red squirrels on the control was 16 percent lower in August 1992 than August 1991, closely matching the 20 percent decrease in adult survivorship from 1991 to 1992. The decrease in survivorship was due to increased predation, implying that predation was primarily responsible for the decline in density and that little demographic compensation (in the form of immigration or juvenile recruitment) for this predation occurred. The very poor survival of neonates in 1992 was the main cause of low juvenile recruitment. Had neonate survival and juvenile recruitment been as high as they were in 1991, the decline in density from March to May due to predation on adults might have almost been completely compensated for. Thus, the decline in density was likely caused by a combination of low survival of adults due to predation and low survival of neonates due to exposure or starvation. However, it is difficult to speculate what the extent of predation on juveniles may have been in 1992 had neonate survival been higher. Juvenile survival was similar in 1991 and 1992, unlike that of adults. One reason it did not decrease in 1992 may have been because there were fewer emergent juveniles in 1992, so that the adult-juvenile ratio was considerably higher than in 1991. If predators hunt red squirrels opportunistically, they would have encountered more adults than juveniles, and predation on adults would have been higher than on juveniles. In addition, the high predation on adults in 1992 left many vacant territories available to juveniles. With the number of emergent juveniles extremely low in 1992, there would have been little competition for these territories, and juveniles may have been able to obtain one without extensive high-risk searching.

Of interest is whether the decline in density represents a significant decline. Other studies on red squirrels have found differences in late summer populations of over 100 percent (Rusch & Reeder 1978), and that the addition of food to a population can cause up to a four-fold increase in density (Klenner and Krebs 1990). In comparison, the 16 percent decline observed in this study appears minor.

Results of this study support a main prediction of the alternative prey hypothesis, namely, that predation on alternative prey species increases as the primary prey declines. The results are also consistent with information on changes in predator diets during a snowshoe hare cycle in central Alberta. Keith *et al.* (1977) found that coyotes, lynx, and great horned owls showed a marked functional (as well as numerical) response to changes in hare densities, with trends in the percent hare biomass in their diet paralleling hare densities. Adamcik, Todd & Keith (1978) reported a marked increase in the consumption of voles, weasels, and red squirrels by great horned owls and red-tailed hawks as hares declined to extreme lows. Studies in this region also showed that great horned owl predation rates on adult ruffed grouse (as determined by analysis of diet) declined from about 5 % in 1966, when hare numbers were very low, to 0 in 1969, and that losses of grouse to owls were very low during the hare peak in 1970-71 (McInvaille & Keith 1974). Rates of predation on grouse by red-tailed hawks were highest also in 1966 and lowest in 1971 (McInvaille & Keith 1974). Conspicuous fluctuations of ruffed grouse have been approximately synchronized with the hare cycle throughout much of North America (Keith 1963), but there is no historical tendency for grouse to decline after hares (Keith 1963). Keith & Rusch (1989) suggest that there is a limit to which hares can buffer predation on grouse, and that this limit is a function of grouse and predator densities, as well as hare densities. As rates of increase and densities of all three groups vary between cycles, grouse may decline before, with, or after hares.

Results obtained in this study are similar to those obtained in experimental studies on small mammals and tetraonids in Sweden. Excluding mammalian and avian predators with fencing produced higher survival in a non-cyclic population of voles (*Microtus agrestis*), and a less pronounced seasonal spring decline in the protected population than in the control population (Erlinge 1987). Similarly, Marcström, Kenward & Engren (1988) reduced mammalian predators on one of two islands in the northern Baltic and found that when predators were present, tetraonid brood sizes and the proportion of females that bred successfully were each positively correlated with vole abundance in summer. When predators were killed, neither of the above variables were correlated with vole abundance. The reduction of predators on one island led to higher brood sizes, higher proportions of females breeding, and higher population sizes than on the island with predators. When predation pressure on boreal grouse during a vole decline was reduced by providing additional food to predators, Lindström *et al.* (1987) showed the proportion of young grouse in autumn was higher on the experimental site than on the control, and that while this proportion decreased on the control relative to the previous year, it did not on the experimental site.

Predation of red squirrels did not increase as 1991 progressed, or in early 1992, despite the continual decline of the hares in 1991 and the relatively high predator densities in that year. This lag in response to changing hare densities has been noted in other studies of alternative prey. Keith & Cary (1991) found a marked decrease in red squirrel populations one to two years after the initial decline of hares from peak abundance, and a similar lag characterized the decline of Franklin ground squirrels (*Spermophilus franklinii*) in Minnesota (Erlien & Tester 1984). Predation was implicated as the primary cause of the declines in both species. In Kluane, the time lag may have been caused by three factors. First, hares declined gradually from peak densities in 1989-90 and were still at relatively high densities in summer 1991. The true 'crash' of the hare population did not occur until winter 1991-92 when numbers declined from 80 to 18 percent of peak. Predator densities also peaked at that time, which resulted in a higher predator-hare ratio, and thus predation pressure on alternative prey, than in previous years.

Second, the presence of other alternative prey species may have buffered predation on red squirrels (Angelstam, Lindström & Widén 1984) to some extent in 1991. Arctic ground squirrel numbers were relatively high in 1991, and there was heavy predation on them that summer (A.Hubbs, pers. comm.). However, vole densities in summer 1992 were considerably higher than in summer 1991 (C.J. Krebs, unpubl. data), and some of the predation pressure on red squirrels in summer 1992 may have been alleviated by voles.

Third, the behaviour of predators likely contributed to the time lag. Hares composed 100 % of the diet of coyotes at Kluane in winter 1990-91 and winter 1991-92 (Appendix II). Coyotes tend to kill many hares in fall and cache them for later use in winter (M.O'Donoghue, pers. comm.), and may have been able to kill enough in fall 1991 to supply them through the winter. In addition, predators may not "switch" directly from primary to alternative prey. The gradual decline of the hares would have allowed a gradual expansion of diet to include other prey species. Keith *et al.* (1977) found that snowshoe hares comprised 77 percent of the diet of coyotes a year after the hare peak, when the hare population was still relatively high. Those authors also found the population decline of lynx, coyote and great horned owl to lag well behind that of the hares, as these predators react to fluctuating prey abundance partly by (numerical) changes in recruitment. There is evidence of this in Kluane as reproduction virtually failed in all predator species in 1992 (Appendix II; C.J. Krebs, unpubl. data). Some avian predators, such as goshawks, may respond numerically more quickly to a decline in their primary prey through migration (Angelstam, Lindström & Widén 1984). The goshawk population in Kluane appears to have peaked in 1990 with the hare population, and has declined in 1991 and 1992 as hares have (Appendix II). The decrease in predator sightings I recorded from 1991 to spring and summer 1992 indicated either fewer predators or a change in predator behaviour. As predator reproduction failed, adult predators did not have to forage to feed their young, perhaps explaining the decrease in sightings.

This study did not continue long enough to determine whether the squirrel population will decline further as hares continue to decline. If predators have switched to red squirrels, predation on squirrels should continue to increase as hares drop to very low numbers, potentially causing squirrel populations to decline significantly over the next years. However, predator numbers are already decreasing due to failed reproduction and movement out of the Kluane valley (Appendix II; see Keith *et al.* 1977), so even if the remaining predators prey exclusively on squirrels, their numbers may be so low as not to affect the squirrel population. However, records of European red squirrel (*Sciurus vulgaris*) densities in Siberia suggest a ten-year cycle of abundance, with no causal relationship to fluctuations in seed crops (Lyobetskaja 1976, in Gurnell 1987). Hare (*Lepus timidus*) populations in the boreal forests of Siberia undergo ten year population cycles (Naumov 1972, in Keith *et al.* 1977) similar to that of snowshoe hares, and it is possible that varying predation pressure is causing the observed cycles in European red squirrels.

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TABLE 2.1. Fates of radio-collared adults, January through August 1992.

			Depredated				collar failure	other
	n	Alive	avian	mammalian	unknown	destroyed		
Control	36	18	7	3	3	4	1	0
Exclosure	24	15	5	0	3	0	1	0

Table 2.2. Survivorship (see text) of adults (from March through August) and radio-collared juveniles (post-emergence to mid September) on each site, each year. Actual survivorship shown in bold, maximum and minimum survivorship (assuming all censored animals to be alive or dead respectively) shown above and below respectively. 95 % confidence intervals in parentheses. Rates followed by the same letter are significantly different by the log rank test, P <.05. Comparisons were made only on actual survivorship within each age class.

	Control	Exclosure
Adults 1991	0.94 (.85-.98) **0.81 (.72-.89)**[a] 0.81 (.72-.89)	0.92 (.84-1.00) **0.73 (.61-.85)** 0.73 (.61-.85)
Adults 1992	0.82 (.75-.90) **0.62 (.53-.72)**[a,b] 0.62 (.53-.72)	0.89 (.80-.98) **0.81 (.70-.92)**[b] 0.81 (.70-.92)
Juveniles 1991	0.67 (.51-.82) **0.66 (.50-.83)** 0.64 (.47-.80)	0.64 (.39-.89) **0.57 (.24-.90)** 0.44 (.19-.68)
Juveniles 1992	0.62 (.46-.77) **0.61 (.44-.77)** 0.51 (.35-.66)	0.67 (.49-.86) **0.61 (.42-.92)** 0.37 (.19-.55)

TABLE 2.3. March body weights (mean and standard deviation) of surviving and depredated squirrels on each site, each year. Sample size in parentheses. See text for discussion of significant differences.

		Survivors	Depredations	Total
Males				
1991	control	283 ±30 (16)	269 ±13 (6)	279 ±27 (22)
	exclosure	275 ±24 (9)	248 ±4 (2)	270 ±24 (11)
1992	control	295 ±19 (11)	280 ±17 (10)	288 ±20 (21)
	exclosure	288 ±15 (11)	307 ±12 (7)	295 ±16 (18)
Females				
1991	control	246 ±21 (19)	262 ±31 (4)	250 ±23 (23)
	exclosure	235 ±16 (12)	262 ±24 (5)	244 ±22 (17)
1992	control	250 ±11 (23)	253 ±20 (21)	252 ±17 (44)
	exclosure	261 ±20 (10)	262 ±6 (4)	262 ±17 (14)

TABLE 2.4. Survival of all juveniles (with and without radios or radio-collars) from birth to ear tagging at 35 days, emergence at 50 days, and to mid September. Percentages shown below absolute numbers. Pairs with the same letter are significantly different (G-tests, $P < .05$). Comparisons made only for similar time periods between sites within years, and between years within sites.

			Survival to : (days)		
Year	Treatment	n	35	50	mid-Sept.
1991	control	60	$60^{a,c}$ 100 %	$55^{b,d}$ 92 %	28^{e} 47 %
	exclosure	23	20^{a} 87 %	17^{b} 74 %	7 30 %
1992	control	114	$41^{c,f}$ 36 %	$31^{d,g}$ 27 %	$18^{e,h}$ 16 %
	exclosure	31	27^{f} 87 %	22^{g} 71 %	14^{h} 45 %

TABLE 2.5. Fates of juveniles that were radio-collared at 50 days (emergence) in 1991, and at 35 days in 1992, through mid September of each year.

			Depredated				Starvation	radio failure
Year	Treatment	n	avian	mammalian	unknown	destroyed		
1991	control	28	1	3	2	1	0	0
	exclosure	12	5	0	0	0	0	2
1992	control	32	2	1	1	2	3	3
	exclosure	21	3	0	2	0	2	5

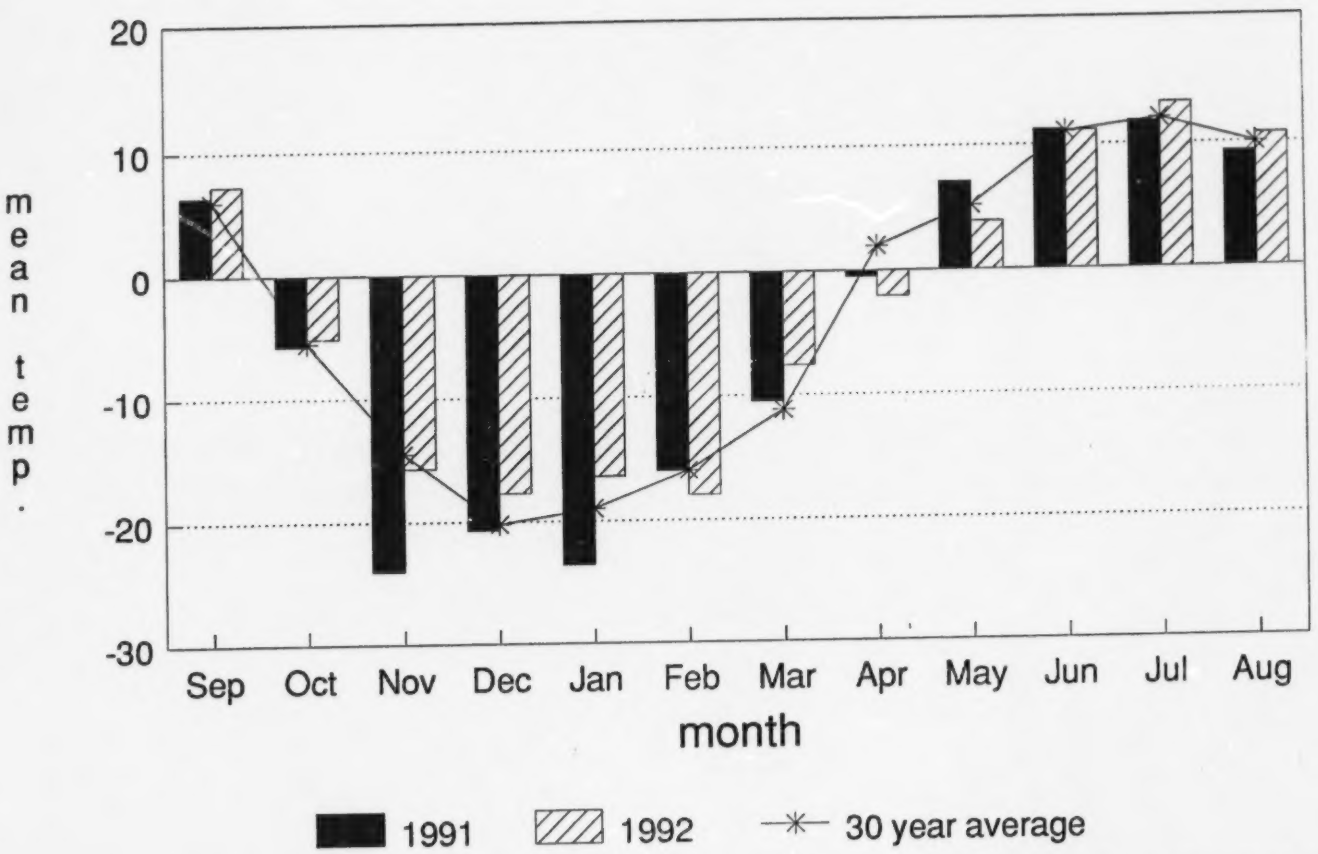

Figure 2.1. Mean monthly temperatures at Burwash Landing, Yukon, in 1991 and 1992, and the 30 year average monthly temperature for each month. (Source: Atmospheric and Environmental Weather Service, Environment Canada, Edmonton, Alberta).

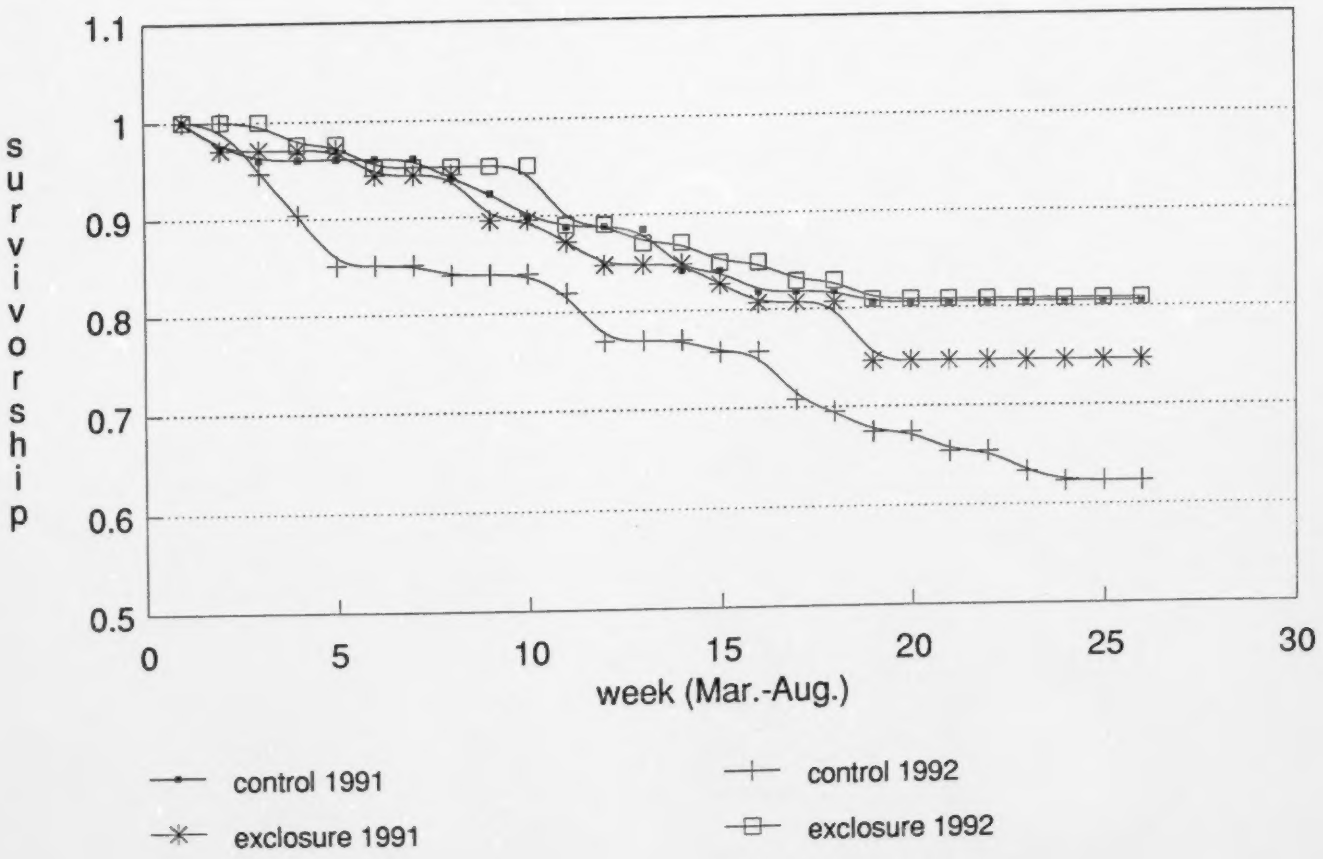

Figure 2.2. Adult survivorship on the predator exclosure and the control site from March through August of 1991 and 1992. Control 1992 lower than control 1991 (LR=6.66, P<.01) and lower than exclosure 1992 (LR=4.56, P<.05).

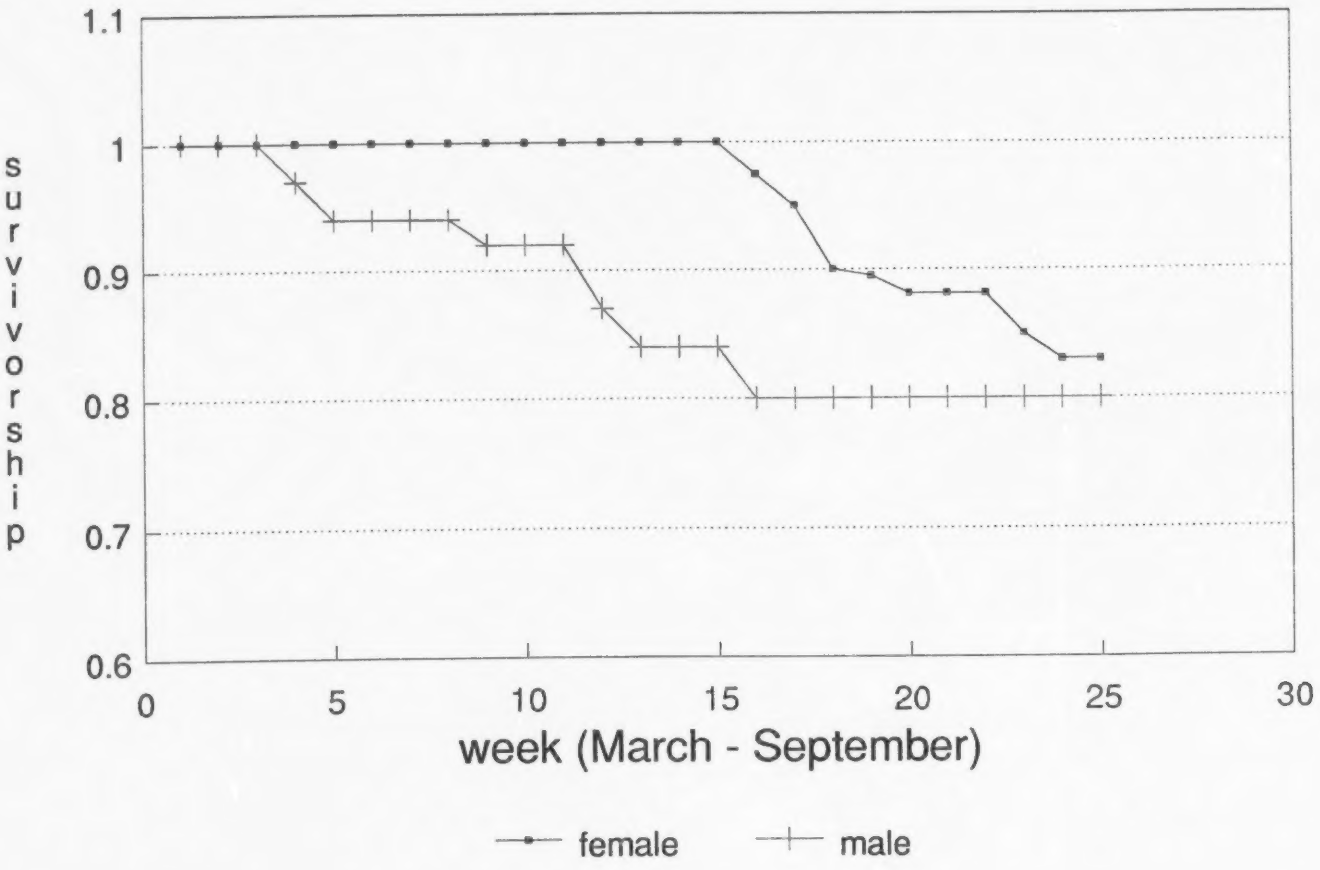

Figure 2.3. Seasonal pattern of male and female survivorship on the control from March through August 1991.

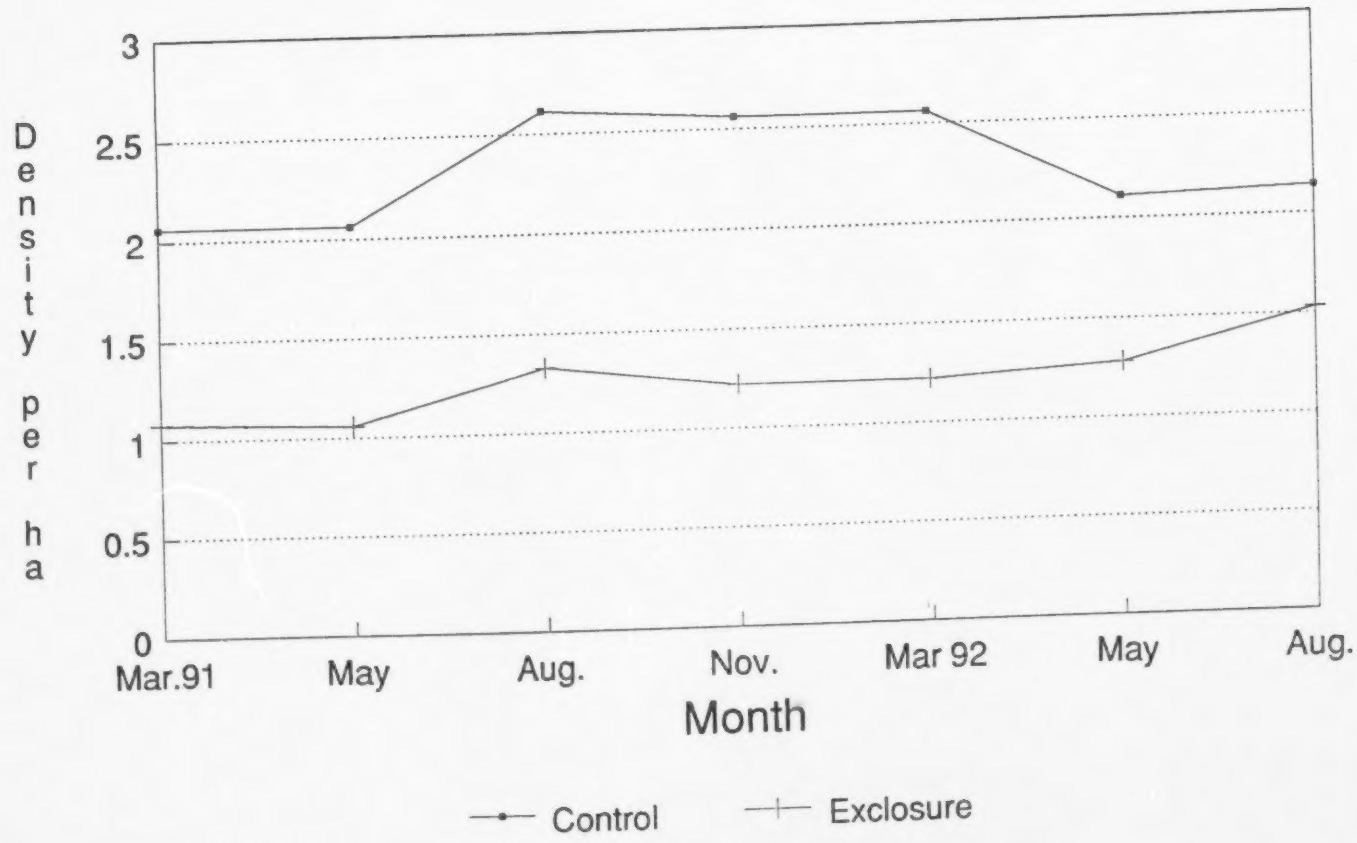

Figure 2.4. Population densities on the exclosure and the control throughout the study.

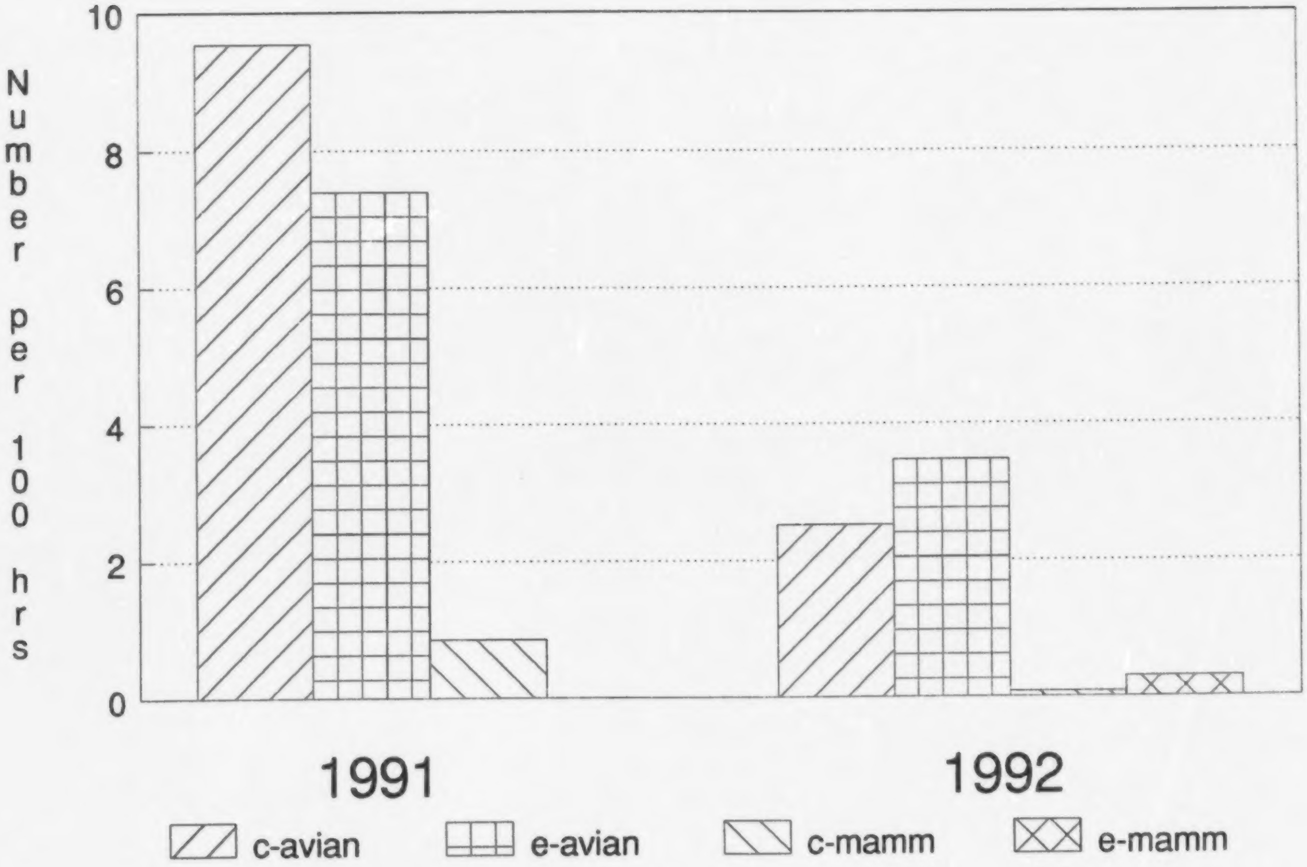

Figure 2.5. Avian and mammalian (mamm) predator sightings per 100 hours on the control (c) and the exclosure (e) in 1991 and 1992.

CHAPTER 3

THE EFFECTS OF FOOD AND PREDATION ON RED SQUIRREL SURVIVAL

INTRODUCTION

Many interacting factors operate simultaneously on populations (Lidicker 1975, in Desy and Batzli 1989). Among them, predation, availability of food, and weather combine to influence population characteristics such as fecundity, survival, and dispersal rates. Most experimental studies of populations in the field, however, manipulate only one factor at a time (Krebs 1988). A single factor approach to population dynamics can lead to misinterpretation of results for a variety of reasons: factors may interact, produce indirect effects, or act sporadically in time and space (Hilborn and Sterns 1982). Thus it has recently been concluded (Taitt and Krebs 1985; Dezy and Batzli 1989), that field manipulations should be designed to test interactions among the various factors.

Predation and the availability of food are important factors that may limit populations of small mammals (e.g. Taitt 1981; Taitt and Krebs 1981; Erlinge *et al.* 1983; Sullivan *et al.* 1983; Sullivan 1990; see Boutin 1990 for a review on the effects of supplemental food). The separate effects of each of these factors have been relatively well-documented through supplemental feeding and predator exclosure experiments, however, their interactive effects remain poorly understood. This chapter reports on an experimental study of the interactive effects of predation and the availability and distribution of food on red squirrels (*Tamiasciurus hudsonicus)* in the northern boreal forest.

The availability of food can affect an individual's physical condition and alter its behaviour, thereby influencing its vulnerability to predation. An animal with adequate food supplies may be less vulnerable to predation than one weakened by starvation (Errington 1956, Keith *et al.* 1984). When food is abundant, short foraging excursions may be adequate to meet nutritional and energetic requirements (Brown *et al.* 1988), and less movement may decrease the risk of predation. When food is less abundant, or scattered in exposed locations, an individual may require longer foraging time, at a higher risk of predation, to satisfy its energetic needs. Optimal foraging studies have shown that foraging decisions may be based on assessment of predation risk as well as foraging efficiency, and that areas of high feeding efficiency may be partially or totally avoided if their use entails greater risks of predation (see Lima and Dill 1990 for a review). Anderson (1986) reported that foraging activity of mice and voles increased in the presence of cover, which presumably reduces risk of predation.

For red squirrels, the availability of food is believed to be the primary factor limiting populations. Red squirrels depend mainly on tree seeds for food, and squirrel populations have been observed to fluctuate with the size of the seed crop (C.Smith 1968, M.Smith 1968, Kemp and Keith 1970) and to quadruple in density when given supplemental food (Sullivan 1990, Klenner and Krebs 1991). The impact of predation on red squirrel populations is not well known. Yearly survival rates have been reported as 40-90 % for adults, and 0-70 % for juveniles, with high seasonal, yearly, and geographic variation (Kemp and Keith 1970, Rusch and Reeder 1978). However, survival measurements rarely separate predation from starvation or death from other causes. Predation may be particularly high in years of low seed abundance, when squirrels are forced to search for additional foods to meet their energetic and nutritional requirements. The lower energetic quality and distribution of these foods (e.g. tree and shrub buds, berries, fungi) may increase the risk of predation when foraging.

The objectives of this study were twofold; to determine 1) if the availability and distribution of food affect predation on red squirrels, and 2) if supplemental food and predation have equal and additive effects on red squirrel survival. My general hypothesis was that protection from predators and provision of supplemental food both increase survival of red squirrels, but that the degree of improvement given by abundant food depends on the distribution of the food. To test this, I first provided supplemental food to individuals in two different ways - one designed to improve physical condition and decrease risk of predation, the other to improve physical condition and increase risk of predation. I predicted that squirrels given supplemental food, regardless of its distribution, would suffer lower mortality due to predation than squirrels without added food, and that squirrels exploiting a scattered and exposed food supply would suffer higher mortality due to predation than squirrels exploiting a clumped and covered food supply. Second, I monitored the survival of individual adult red squirrels on four sites; a predator-exclosure, a food addition, a predator exclosure with food addition, and a control. If predation and supplemental food have equal and additive effects on survival, populations with both supplemental food and protection from predators should show the highest survival, populations with either supplemental food or protection from predators should show intermediate survival, and populations with neither factor should show the lowest survival. If food and predation have interactive effects on adult survival, squirrels on sites with additional food may have a higher or lower risk of predation than squirrels on sites without additional food, and survival may be lower or higher respectively on sites with additional food, than on control sites. Results from the first experiment, performed at the level of the individual, should aid in interpreting results from this experiment, at the level of the population.

METHODS

The study was conducted in the Shakwak valley near Kluane Lake, south-west Yukon from May 1991 through August 1992, in conjunction with the Kluane Boreal Ecosystem Project. All sites except one (Heaven) used for the study were established by the project. A more detailed description of the study area is given in Chapter 1. Cone production of the dominant conifer, white spruce (*Picea gluaca*), was measured on each of the sites in August 1990 and again in August 1991 (Appendix IV). The cones produced in August of each year, depending on the size on the crop, form the basis of the red squirrels' food supply over winter and into the summer of the next year.

Experiment 1

The purpose of this experiment was to determine the effect of the distribution and abundance of supplemental food on the behaviour and survival of red squirrels. The experiment was conducted from 1 May through 31 July 1991 on four sites of similar habitat (Sulphur, Kloo, Lloyd, and Heaven). Each site was dominated by young white spruce and was fairly open, with little understory (mainly willow, *Salix spp.*). Sulphur (40 ha) and Kloo (20 ha) were located directly across the Alaska Highway from each other, Lloyd (40 ha) was 2 km east on the same highway, and Heaven (20 ha) was situated off the old Alaska Highway, approximately 3 km south-east of Lloyd. Sulphur and Heaven were very similar; both sites were dominated by spruce of the same size (pers. obs.), contained no patches of aspen (*Populus tremuloides*), had a road and pipeline running through them, and had a similar density of red squirrels (unpubl. data). All predator sightings and the total hours worked were recorded for each site.

Only breeding females were used in this experiment. Lactation in squirrels demands up to four times baseline (non-reproductive) energy (Havera 1979), and thus breeding females were presumed more likely to respond to supplemental food than males or non-breeding females. On each site in late April 1991, traps were set at middens and opened for one to two hours per session for several sessions, until all resident females were uniquely colour tagged and their middens identified. Resident red squirrels show high territory fidelity and give territorial 'rattle calls' to show ownership (C.Smith 1968). Three of the sites (Sulphur, Kloo and Lloyd) were already in use as part of a long term study on red squirrels by S.Boutin, and the middens of resident females were known. Each breeding female was assigned to one of three treatments described below; food-exposed, food-cover, or control. Due to logistical constraints, food-cover females and their controls were located on Kloo and Lloyd (treatment and control squirrels on each site), while all food-exposed females were located on Heaven, and their controls situated on Sulphur. Treatments were applied from 1 May through 31 July 1991. Females were trapped weekly during this time period and their weight and reproductive condition determined (as in Chapter 2). The percent change in body weight from parturition to weaning of the litter was calculated for each female and compared among treatments to determine if the addition of supplemental food improved physical condition. Survival was monitored weekly through trapping or observation. Adult red squirrels are very sedentary and squirrels missing from their territories for more than three weeks can be considered dead (Chapter 2).

Treatments

Food-Exposed - This treatment was designed to improve physical condition and increase risk of predation, by inducing squirrels to feed while exposed to predators. Females assigned to this treatment were provided with two feeders in clearings of at least 4 m in diameter, no further than 10 m from their midden. Preliminary experiments showed that feeders further than 10 m were often used by neighbouring squirrels. Each feeder consisted of a tin can (10 cm deep, 12 cm diameter), with a hole three cm in diameter cut in one side and a securely fitting lid, nailed to a 1 metre high wooden stake. This design allowed squirrels to climb the stake and obtain food from the can, while preventing birds and ground squirrels from doing so. Feeders were filled with 175 grams of sunflower seeds twice per week such that each squirrel received an average of 100 g of seeds per day. Sunflower seeds contain 24 kJ/g (in Becker 1992), so each female received 2400 Kj/day, more than enough to satisfy the requirements of lactating females (2200 Kj, assuming the normal daily energy expenditure of a squirrel to be 2.2 Kj/g/day at 20 C (C.Smith 1968), an average weight of 250 g, and the energy requirement of a lactating female squirrel to be four times that of a non-lactating squirrel (Havera 1979)).

Food-Cover - This treatment was designed to improve physical condition and decrease risk of predation, by inducing squirrels to feed under cover. Females in this treatment were provided with one tin can (15 cm deep by 10 cm diameter), with a hole 3 cm in diameter cut in one side, wired to a nest tree on their midden. The feeder was placed at least 1.5 m above the ground and covered with branches. Each feeder was filled with 350 g of sunflower seeds twice per week, so that females received an average of 100 g of seeds per day, as for the food-exposed treatment.

Control - Females in the control group were neither given sunflower seeds nor manipulated in any way. These squirrels were also visited twice per week (at least) by workers involved in another study (by S.Boutin) on red squirrels.

Behavioral observations

To ensure that the treatments were altering behaviour and exposure to predators, the behaviour of 15 squirrels, five randomly selected from each of the three treatments, was observed. Each selected female was observed for three, 45 minute periods between 5 May and 25 May 1991. Red squirrels habituate quickly to observers (Price *et al.* 1986), and each female was observed for at least two, 15 minute periods before recorded observation began. Observations were made only during times the squirrels were most likely to be active (7-11 am, 7-10 pm, pers. obs.), and activities were recorded on a portable computer programmed with 'The Observer' (Noldus Information, University Business and Technology Center, Vadaring 51, 6702 EA Wageningen, The Netherlands). Behaviour and spatial location were recorded simultaneously and continuously. Six independent behaviours and eight independent spatial locations were defined. The computer was configured such that each behaviour and each location corresponded to a particular key, which was pressed when that event occurred. Behaviours included: eating/foraging (actual eating, handling, caching, or searching for spruce buds in the tree tops, digging in the ground or midden, moving slowly with nose to the ground, or otherwise apparently searching for food), resting (generally motionless, usually on a branch or in the nest, includes grooming), travelling (moving directly across the ground or trees), vigilant (silent, head up, often standing on hind limbs), interactions with other squirrels (chasing, being chased), and rattling (an aggressive, territorial call). There was also an out-of-sight/behaviour unknown category. Spatial locations were designated so as to differentiate between exposed and covered locations. Categories included: in nest, tree-exposed (on the tips of branches, further than 1 m from the trunk or at the tree top and easily seen by an observer), tree-cover (within 1 m of the trunk, hidden by branches and difficult to see), ground-exposed (in a clearing out from under the canopy of a tree, more than 2 m from the tree trunk), ground-cover (on the ground under the canopy of a tree no more than 2 m from the tree trunk), feeder-exposed (feeding from the exposed feeders, exposed-food treatment only), feeder-cover (feeding from the covered feeders, covered-food treatment only), and out-of-sight.

The duration (in seconds) and frequency of occurrence of each event was determined using the analysis package from 'The Observer'. The proportion of time spent exposed to predators (regardless of behaviour) was calculated for each observation as total time spent exposed divided by (the total time subtract time out-of-sight) and transformed with an arc-sine transformation (Sokal and Rohlf 1981). Time exposed was compared among treatments with an ANOVA and orthogonal comparisons (Sokal and Rohlf 1981).

Experiment 2

The objective of this experiment was to determine if provision of supplemental food over winter improves survival of adult red squirrels. As resources for purchasing food were limited, and males and females show different seasonal patterns of survival (males experience most mortality in spring, females in summer, Chapter 2), only one sex (females) was selected to receive food, so that sample size could be kept relatively high.

Twenty adult females on Heaven were individually supplied with sunflower seeds from November 1991 through April 1992. Seeds were provided in buckets (50 *l*) with tightly fitting lids and a small hole near the bottom, placed such that the hole connected with an existing tunnel in the midden and was hidden by a large piece of deadfall. Buckets were filled with 6 kg of seeds in early November and 3.05 kg in early March, such that each squirrel received an average of 50 g (1200 Kj) per day from 1 November 1991 through 31 April 1992. There are no published data on energy requirements of squirrels at temperatures other than 20° C, so the requirement for a 250 g squirrel at this temperature (550 kJ, C.Smith 1968) was approximately doubled to account for colder temperatures. Squirrels were enumerated in early November, March, and May by trapping at middens until the owner was caught or determined absent (not trapped in four trapping sessions or sighted on the study site). The proportion of females surviving from November 1991 through February 1992 and from March through April 1992 was determined, and compared to the survival of females without supplemental food on a control site (Sulphur).

March body weights of food supplemented and control females were compared to determine if physical condition improved with supplemental food. Body weights in May could not be compared as female body weights at this time are affected by pregnancy and lactation.

Experiment 3

The purpose of this experiment was to determine if supplemental food and protection from predators have equal and additive effects on red squirrel survival. Four sites (each 40 ha) were used for this experiment, a food addition (Gravel pit), terrestrial predator exclosure (Beaver Pond), food addition plus terrestrial predator exclosure (Hungry Lake), and unmanipulated control (Sulphur). Food addition sites received 290 kg of Purina rabbit chow every four days, distributed down four trails running through the sites at equal intervals. Although the food was originally provided for snowshoe hares, red squirrels have been observed eating the chow (S.Boutin, pers. obs.). It is not known, however, how much they consume. Each predator exclosure site was located within a separate 1 km^2 area enclosed by a 2 m high electric fence that effectively excluded most mammalian predators. A minimum of 20 resident adult red squirrels were trapped, weighed and fitted with numbered ear tags (if not already tagged) at middens on each site in late August 1991. All middens on food addition grids were located within 20 m of a food distribution trail to ensure that the owner had access to the food. Squirrels were trapped at middens again in early June and late August 1992 and the proportion of adults surviving through each time period determined. Body weights of adults in August 1991 and August 1992 were compared among sites by year.

RESULTS

Experiment 1

The white spruce cone crop was moderately heavy in 1990 (Appendix IV), ensuring a good food supply for squirrels during winter 1990-91 and spring 1991. Female squirrels on all sites were observed eating cones from this crop in May and early June 1991. Predators were seen on all sites, with more predator sightings per 100 hours on Sulphur than on Heaven (Figure 3.1). The majority of the predators seen were northern goshawks (*Accipiter gentilis*) and Harlan's hawks (*Buteo harlanii*).

Behaviour

Squirrels used the feeders readily. Squirrels given feeders attached to their nest tree (food-cover treatment) extracted seeds from the can and sat on top of the can or on a nearby branch to eat the seeds. They were observed plugging the hole in the feeder with grass or shredded bark, but were never seen removing the seeds from these feeders and caching them elsewhere. Squirrels given feeders on stakes (food-exposed treatment) climbed up the stake, stuck their head in the hole and extracted seeds one at a time. They would then either sit on top of the can and eat the seed, climb down the stake and eat the seed on the ground, travel to the cover of a nearby tree and eat the seed, or cache it in their midden or a nearby tree. Females were observed feeding in 41 of the 45 observations. Squirrels in the food-exposed group (n=18) spent an average of 57±14% of their total time observed at the feeder, and squirrels in the food-cover group (n=24) spent 61±30 % (two-tailed *t*=.56, df=40, P>.5).

As observations were collected randomly during the three week period (i.e. not all squirrels were observed on the same day, or even within a period of days), it was not possible to perform repeated measures analysis on the data, or even to block by day to control for day effects. Thus, the three measures of proportion time spent in an activity for each individual were averaged, and the averages analyzed with an ANOVA. Many averages fell outside the 30-70 % range, so they were transformed with an arc-sine transformation (Sokal and Rohlf 1981) before analysis. The variation within and among individuals is less than that among treatments (Figure 3.2). The proportion of time females spent in exposed locations differed significantly among treatments (ANOVA, F = 17.54, df=2,12, p < .001, Figure 3.3). Females in the food-cover treatment spent less time exposed than females in the food-exposed treatment (F = 25.9, df=1,12, p <.0003) or the control (F = 26.3, df=1,12,p <.0002), but there was no difference between food-exposed treatment and the control (F = 0.005, df=1,12,p >.05).

The proportion of time spent feeding did not differ among treatments (food-exposed 0.64±.11, food-cover 0.68 ±.5, control 0.73 ±.14, F = 1.027, df=2,12, p=.388).

Weight

The average percent body weight change of adult females from parturition to weaning was used as a measure of the effect of supplemental food on weight. As the food-cover treatment and controls were replicated on Kloo and Lloyd, these two sites were analyzed with a two-way ANOVA, blocking on site to remove variation due to site. There was no effect of treatment (F=0.88, df=1,25, p=.357), but a significant effect of the block (F=19.35, df=1,25, p=.0002). However, there was no difference in percent weight change for control females on Kloo, Lloyd, or Sulphur (one-way ANOVA F=1.46, df=1,27, p=.25). Weight changes of food-exposed females on Heaven and control females on Sulphur were compared with a one-way ANOVA, which again, showed no difference due to treatment (F=.25, df=1,32, p=.62). Females on Lloyd, Sulphur, and Heaven all experienced an average weight loss over lactation, but on Kloo, both control and food-cover females gained weight (Figure 3.4). This weight gain was not significantly different between control and food-cover females (two-tailed t=1.67, df=7, p=.16), however, and small sample sizes on Kloo make conclusions tenuous. In general, the above analyses show no effect of supplemental food on weight change over lactation.

Survival

There was no difference in survival among treatments and controls on any of the sites (G= 5.36, df=7, p=.62, Figure 3.5). Not was there any difference when all squirrels in each treatment were combined; food-exposed squirrels (n=18) had 78% survival, control squirrels (n=41) 83 % survival, and food-cover squirrels (n=24) 92 % survival (G=1.68, df=2, p=.43).

Experiment 2

There was no difference in survival of adult females on the site with supplemental food versus the control from December 1991 through February 1992 (G = 2.43, df=1, p=.518), or from March through April 1992 (G=0.418, df=1, p=.518)(Figure 3.6). Most seeds buckets were empty in early March, though two still contained about 20 % of the seeds, and most contained dried fungi, presumably cached by the squirrels. The presence of large piles of sunflower seed shells near the seed buckets indicated squirrels, and not resident gray jays (*Perisoreus canadensis*) or chickadees (*Parus hudsonicus* and *Parus atricapillus*), had been eating the seeds. These birds were never observed shelling the seeds, and on the few occasions they were seen taking them they flew at least 5 m away and either cached or ate the entire seed.

The March body weights of food-add (255 ±20, n=17) and control females (252 ±17, n=39) were not significantly different (one-tailed t =.527, df= 54, p=.300).

Experiment 3

There was no significant difference in adult survival among the four sites from August 1991 through mid-June 1992 (G=5.311, df=3, p=.19) or from mid June through August 1992 (G= 5.064, df=3, p=.17), although squirrels with protection from mammalian predators tended to show higher survival than those with supplemental food (Figure 3.7).

The average August body weights of adult squirrels were similar among sites in both years (year F= 3.463, df=3,54, p=.064, site F=.349, df=3,54 p=.790), although the p value for year suggests a tendency toward higher body weights in 1992, at least on one site (Figure 3.8).

DISCUSSION

Did the distribution of supplemental food affect survival ?

It is most likely that, in this study, all squirrels presumed dead were depredated, rather than dead from starvation or other causes. In a concurrent radio-telemetry study of adult red squirrels in the same area, all of the squirrels that died were depredated, and no evidence of starvation or disease was found (Chapter 2). The behavioral observations from experiment 1 suggest that, if foraging in exposed locations carries a high risk of predation, squirrels in the food-cover treatment should have shown higher survival than squirrels in either the food-exposed or control treatments. Survival was similar in all treatments, however, suggesting that feeding in exposed locations does not carry a high risk of predation. Squirrels may not be vulnerable when feeding, as they can often scan for predators while eating or foraging (Lima *et al.* 1985), unlike small birds such as sparrows (Lima 1989). Rather, they may be most vulnerable when engaged in other behaviours such as territorial defence or mating chases. However, there is evidence that animals assess the prevailing risk of predation in deciding when, where, and how to forage (Lima and Dill 1990). In an experimental study by Brown *et al.* (1988), small desert rodents almost completely avoided the open in response to the presence of barn owls, an appropriate response considering that predation by barn owls was higher in the open microhabitat. Yahner (1987) found that primary feeding sites of red squirrels in Pennsylvania had greater densities of understory than did secondary sites, and suggested that dense understory trees provide protection from avian predators. In addition, foraging studies on grey squirrels (*Sciurus carolinensis*) have shown that squirrels trade-off energy intake rate against predation risk (Newman and Caraco 1987; Newman *et al.* 1988) and that behaviour while foraging is strongly dependent on distance to cover (Lima *et al.* 1985; Lima and Valone 1986). Thus, if squirrels were acting to minimize their predation risk while foraging, the amount of time exposed would have to be increased, rather than decreased, to decrease survival. The food-exposed treatment did not increase time spent exposed over that observed for the control squirrels. Alternatively, as squirrels did increase their foraging time in the open, predation risk may have been very low. This idea is supported by the high survival rate of squirrels in the control treatment.

The period when supplemental food was available may have been too brief to affect predation rate on the squirrels, or sample sizes too low to detect a response. Survival of squirrels on the control was very high from May through July 1991, and detecting an improvement would have been difficult without very large sample sizes. When replicates were combined and sample size thereby increased there was a tendency for squirrels in the food-exposed treatment to show the lowest survival, squirrels in the control to show intermediate survival, and squirrels in food-cover the highest survival.

The observed behaviour is consistent with that seen in other studies, despite the small number of behaviour samples taken. The proportion of active time females spent feeding (64-73 %) is similar to that reported for lactating female red squirrels (58-65 %, C.Smith 1968), and for European red squirrels (*Sciurus vulgaris*) (62-73%, Wauters and Dhondt 1987). Squirrels in the food-cover treatment spent 60 percent of their foraging time at the feeders, indicating they spent about .7 x .6 = 42 % of their total time active feeding under cover. This behavioral change likely extended to non-observation periods, as observation times were chosen at random and the squirrels used the feeders in each observation.

Did supplemental food improve survival ?

Provision of supplemental food did not have any measurable effect on survival of adult red squirrels during the winter of 1991-92, or the summers of 1991 or 1992. This agrees with findings of other food addition studies on red squirrels (Sullivan and Sullivan 1982; Sullivan 1990; Klenner and Krebs 1991; Larsen 1992) that found no consistent increase in survival with provision of supplemental food, and with the results of Koprowski (1991) who reported no difference in adult survival of grey squirrels between abundant and poor (mast failure) food years. Food addition to populations of small mammals does not, overall, increase adult survival (Boutin 1990). Sullivan and Sullivan (1982) reported higher overwinter survival of females in a population of red squirrels (*Tamiasciurus douglasii)* with supplemental food, but their sample size was very low. Other food addition studies on mammalian populations showed that over winter survival was improved in 7 of 16 cases (Boutin 1990).

I expected supplemental food to increase survival over the winter of 1991-92, as there was a virtual cone failure over the study area in fall of 1991, and red squirrels require a cache of stored food to survive the winter (C.Smith 1968; M.Smith 1968; Kemp and Keith 1970). Yet female survival during this winter was 100 percent in the control population, suggesting that food was not limiting. During the winter, squirrels were observed clipping shoots from spruce trees and eating the meristematic and cone buds in great numbers. White spruce cones are initiated 18 months before maturation, and the buds differentiate the summer preceding the crop (Owens and Molder 1981). As the cone crop in 1992 was moderately heavy, immature cone buds would have been present in high numbers, offering a protein rich food source (Kramer and Kozlowski 1960, in Kemp and Keith 1970) to the squirrels. Kemp and Keith (1970) and C.Smith (1968) observed higher overwinter survival and increased rates of reproduction immediately before a medium-to-heavy cone crop, which Kemp and Keith (1970) attributed to the presence of large numbers of spruce buds. In addition, fungi production appeared very high in the summer of 1991, and the presence of dried fungi in the seed buckets indicate squirrels were using them as a winter food. Fungi contain approximately the same amount of protein as spruce seeds, as well as several other important nutrients (Grönwell and Pehrson 1984), and this resource may have been very important in winter 1991-92. Thus food supply was likely good during the winter of 1991-92. Boutin (1990) concluded that populations are less likely to respond to supplemental food when environmental conditions are fair to good than when they are poor.

It is possible that supplemental food influences survival of juveniles more than adults. Koprowski (1991) reported survival of juvenile gray and fox (*Sciurus niger*) squirrels to be lower in the year of a fruit failure, but that adult survival remained high. We followed juvenile survival from birth to 50 days, but found virtually 100 percent survival of young born to both food add and control mothers in 1991 (unpubl. data). In 1992, however, 53 percent of the control mothers lost their litters entirely and many neonates died before reaching 50 days (Chapter 2). This was likely due to lack of food and very cold temperatures in May (Chapter 2), suggesting that a certain abundance of food is required by lactating mothers for neonate survival. Sullivan and Sullivan (1982) found juvenile survival of red squirrels (*Tamiasciurus douglasii)* to be higher in a population with supplemental food. However, they did not monitor individual survival and the apparent increase may have been due to lower juvenile dispersal in the population with supplemental food. In addition, they calculated juvenile survival through a modified Krebs index relating recruitment of young to the number of lactating females. As there was a very high relative number of lactating females in the population with supplemental food, and they did not measure litter size, which may have been higher in populations with supplemental food (Larsen 1992), this index may have been biased in food populations. Many studies have directly (through measurements of cone crops and squirrel populations) or indirectly (through food additions) concluded that red squirrel populations fluctuate in accordance with the abundance of food (C.Smith 1968, Kemp and Keith 1970, Sullivan and Sullivan 1982, Sullivan 1987, but see Rusch and Reeder 1978). The observed increase in density following mast crops is probably due largely to increased immigration, and improved juvenile recruitment (Klenner and Krebs 1991), rather than increased adult survival.

Did supplemental food increase body weights ?

I expected body weight to remain stable or increase when supplemental food was provided to individual lactating females, as lactation demands four times baseline energy (Havera 1979), and females have been observed to lose weight during lactation (Boutin, unpubl. data). The body weights of adults increased with food addition in the majority of food supplementation studies reviewed by Boutin (1990). I observed females eating the majority of the sunflower seeds they were given, and their seed containers were usually empty when I came to refill them. However, there was no significant increase in body weight over lactation with supplemental food. This result agrees with Larsen (1992), who found no difference in weight change over lactation between females with added cones and those without, and with Klenner and Krebs (1991), who reported no change in weight of females over summer when they provided supplemental food to a red squirrel population in British Columbia.

Sunflower seeds contain 22 % protein and a similar amount of caloric energy to spruce seeds (in Becker 1992). Becker (1992) showed that sunflower seed additions to female red squirrels over winter resulted in earlier oestrous dates and thus earlier parturition, and Larsen (1992) found similar seed additions to produce proportionately more litters in the larger size classes. This suggests that females channelled the extra energy provided by the seeds into reproduction, rather than body mass. In a food addition experiment on Columbian ground squirrels (*Spermophilus columbianus*), Dobson and Kjelgaard (1985) found that the amount of energy invested in reproductive effort increased in the food-supplemented populations, as compared with control populations. I did not measure reproduction or litter size in the population that was fed over winter, but on one food addition site (Heaven) in summer 1991, females were fed before it was confirmed that they were pregnant. Eighty-five percent of females bred there, whereas only 55 percent bred in the control population (unpubl. data). The average birth date was later and the range of birth dates wider (unpubl. data) on Heaven, suggesting that the additional food allowed some females to breed that might not have done so otherwise.

Do protection from predators and supplemental food have equal and additive effects on survival ?

Protection from predators improved adult survival more so than supplemental food, and equally well or better than protection plus supplemental food. This agrees with results of the previous two experiments that found no effect of supplemental food on adult survival.

It is possible that squirrels were not using the supplemental food provided on the sites, or that the rabbit chow was not of high enough quality to enhance survival. Purina rabbit chow contains between 14-18 % crude protein, and allows microtines to grow and reproduce well (Cole and Batzli 1978), though there have been no published studies of its effects on squirrels. On Hungry Lake, the high ground squirrel (A.Hubbs, pers. comm.) and high hare densities (Appendix I) may have resulted in severe competition for the chow, with the result that squirrels got very little.

The population density of snowshoe hares, which differed among sites (Appendix I), may have confounded the effects of food and protection from predators on squirrel survival. Depredation of squirrels on the control was higher when hare densities were lower (Chapter 2), so predation rates may have differed among sites. In addition, the density of predators may have varied among sites. I have no measure of predator use of each of the sites, however, in summer 1992 Harlan's hawks and lynx were often seen on Gravel Pit (A.Hubbs, pers. comm.), whereas these predators were rarely seen on Sulphur (Chapter 2). This may explain the slightly lower survival on Gravel Pit than on the other sites in summer 1992.

The results of this experiment are consistent with results of a similar factorial manipulation of food and predation on small mammals (Dezy and Batzli 1989, Dezy *et al.* 1990), that found protection from predators, but not extra food, generally improved survival of adult prairie voles (*Microtus ochnogaster*), and that there was no interactive effect of food and predation on adult survival. The one other published experimental study of food and predation on small mammals (Taitt *et al.* 1981), was performed on a population of voles (*Microtus townsendii*) during the annual spring decline in numbers. Voles on the area with extra cover had the highest survival, and the rate of decline on this site was significantly lower than on control sites.

I found no obvious interaction between food availability and predation in this experiment, however, only survival was measured. Desy and Batzli (1989) reported a significant interaction in that the presence of predators appeared to inhibit the growth response of prairie voles to supplemental food, possibly because of restricted movement and thus less access to food. Desy and Batzli (1989) also found that food supplementation and protection from predators generally had equal and additive effects on vole density. In addition, exposure to predation appeared to reduce home range size, which Dezy *et al.* (1990) concluded was probably a direct behavioral response of voles to the presence of predators. Taitt *et al.* (1981), reported an interesting effect of extra cover in that breeding was earlier, and the proportion of breeding females higher, in vole populations with extra cover. However, they attribute this effect to the increased complexity of the surface vegetation with added cover (straw), which may have reduced the rate of encounter of female voles, thereby increasing their reproductive rate (Taitt 1981). It is possible the above interactions occur in red squirrel populations as well, and future studies should measure responses other than survival to manipulations of food and predation.

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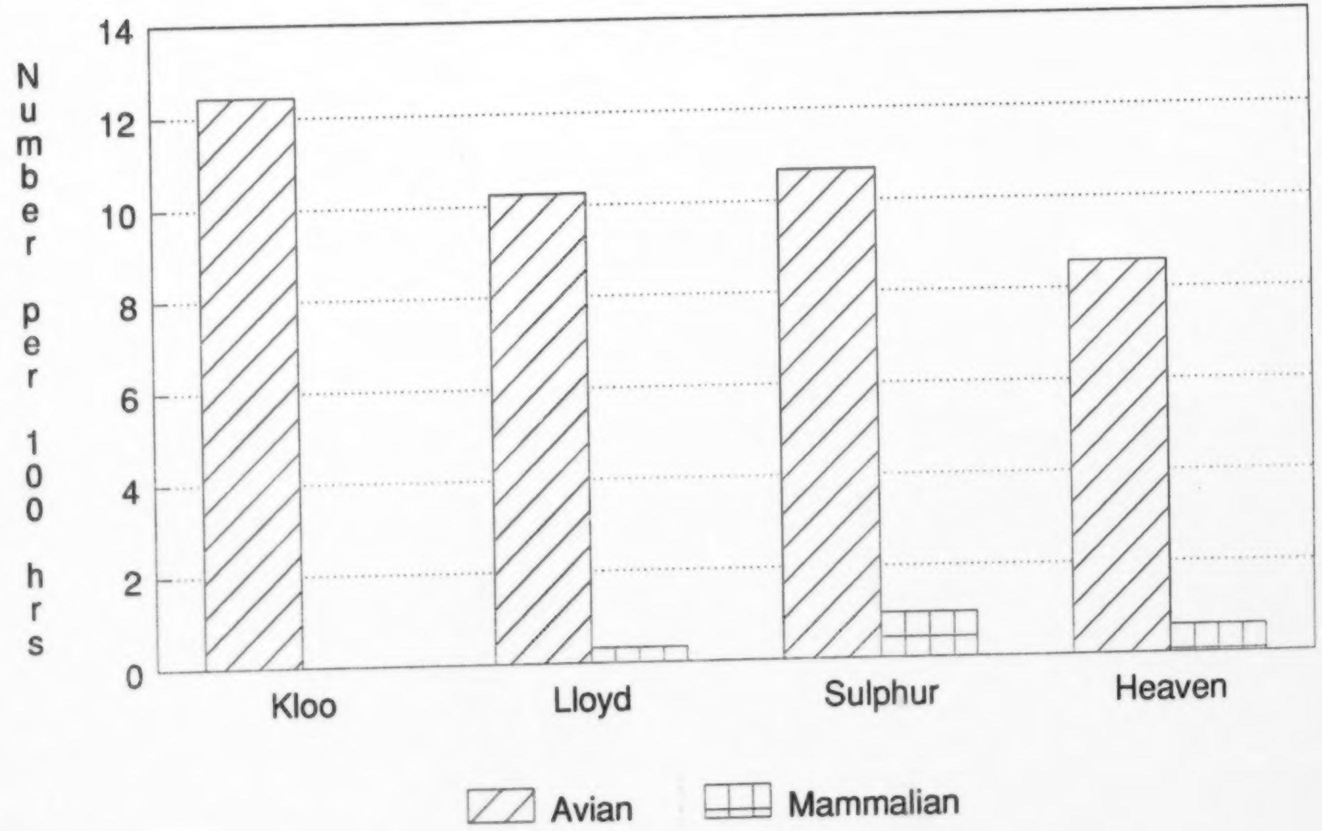

Figure 3.1. Predator sightings per 100 hours on each site from May through July 1991.

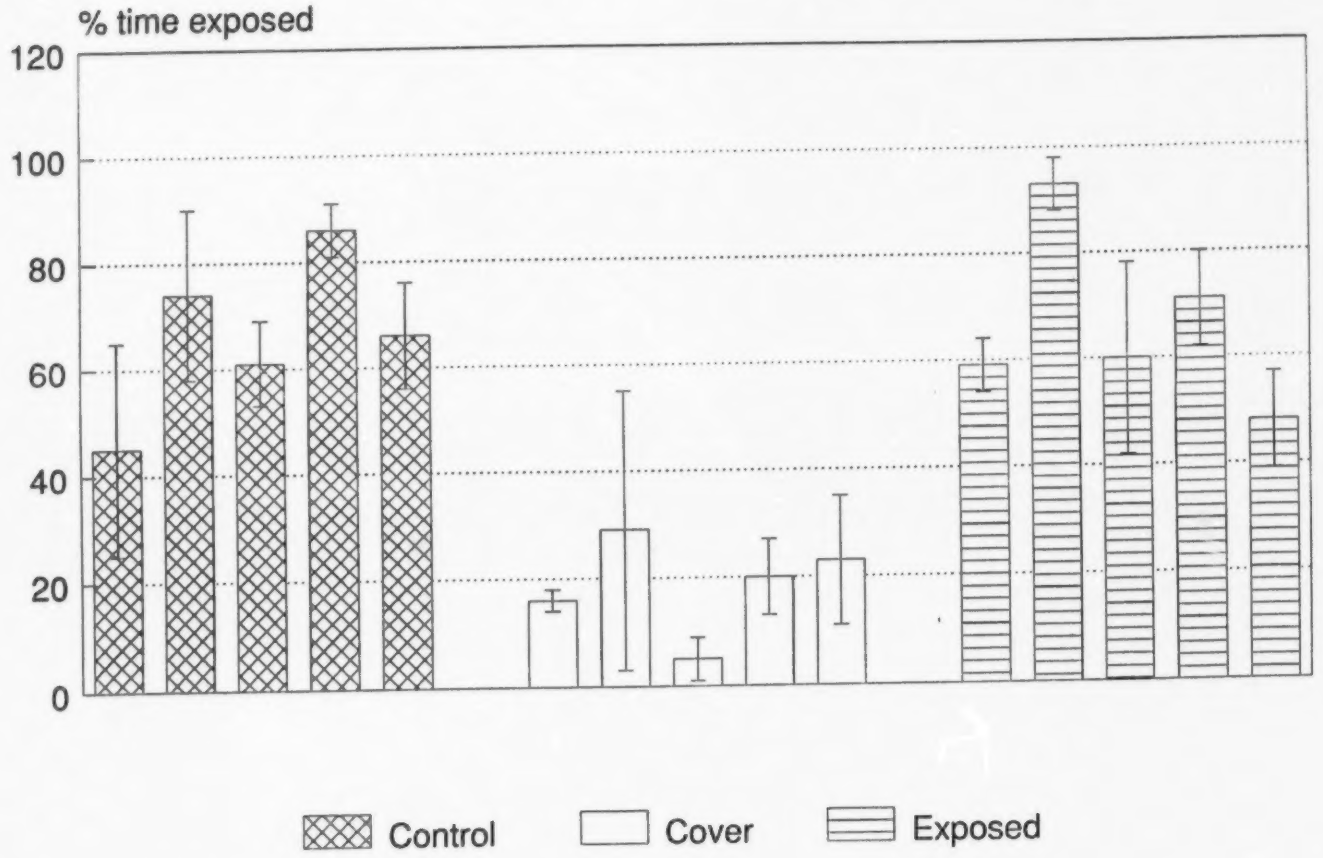

Figure 3.2. Mean percent (and s.d.) of time spent exposed to predators for each of the five females in each treatment.

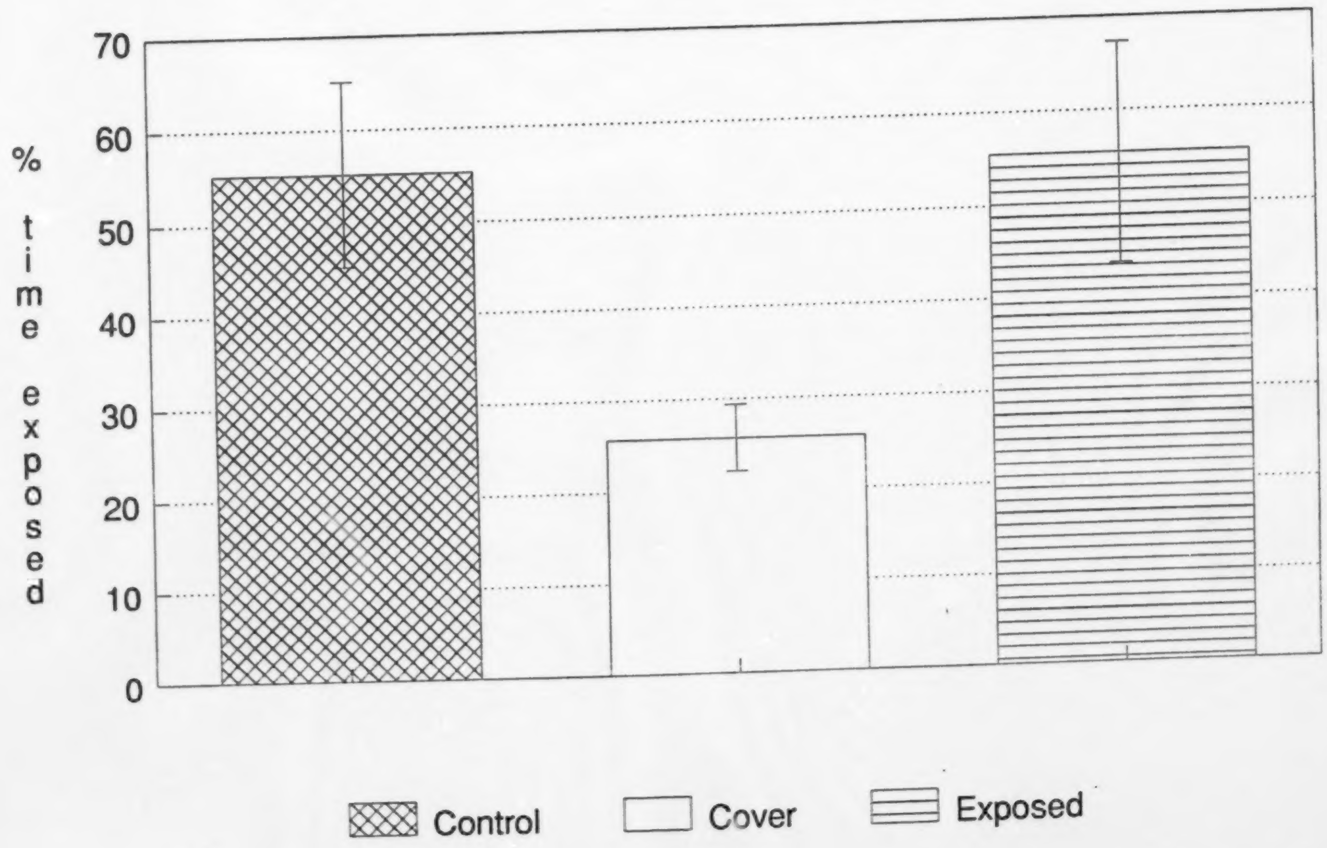

Figure 3.3. Average (and s.d.) proportion of time females in each treatment spent exposed to predators. Cover significantly lower than control (F=26.3, P<.0002) and exposed (F=25.9, P<.0002).

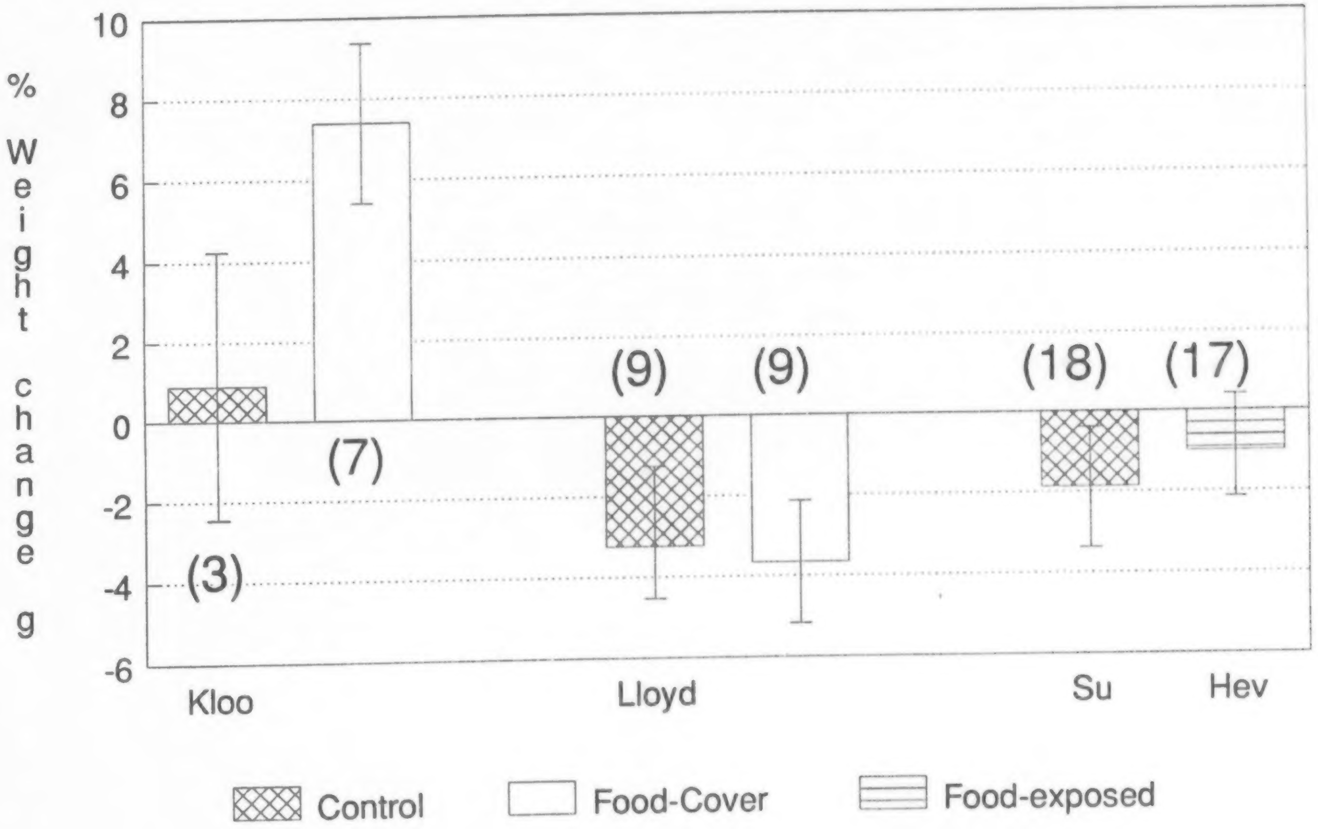

Figure 3.4. The average percent body weight change and standard error from parturition to weaning for females on each site. Sample size in parentheses. No significant differences among sites or treatments.

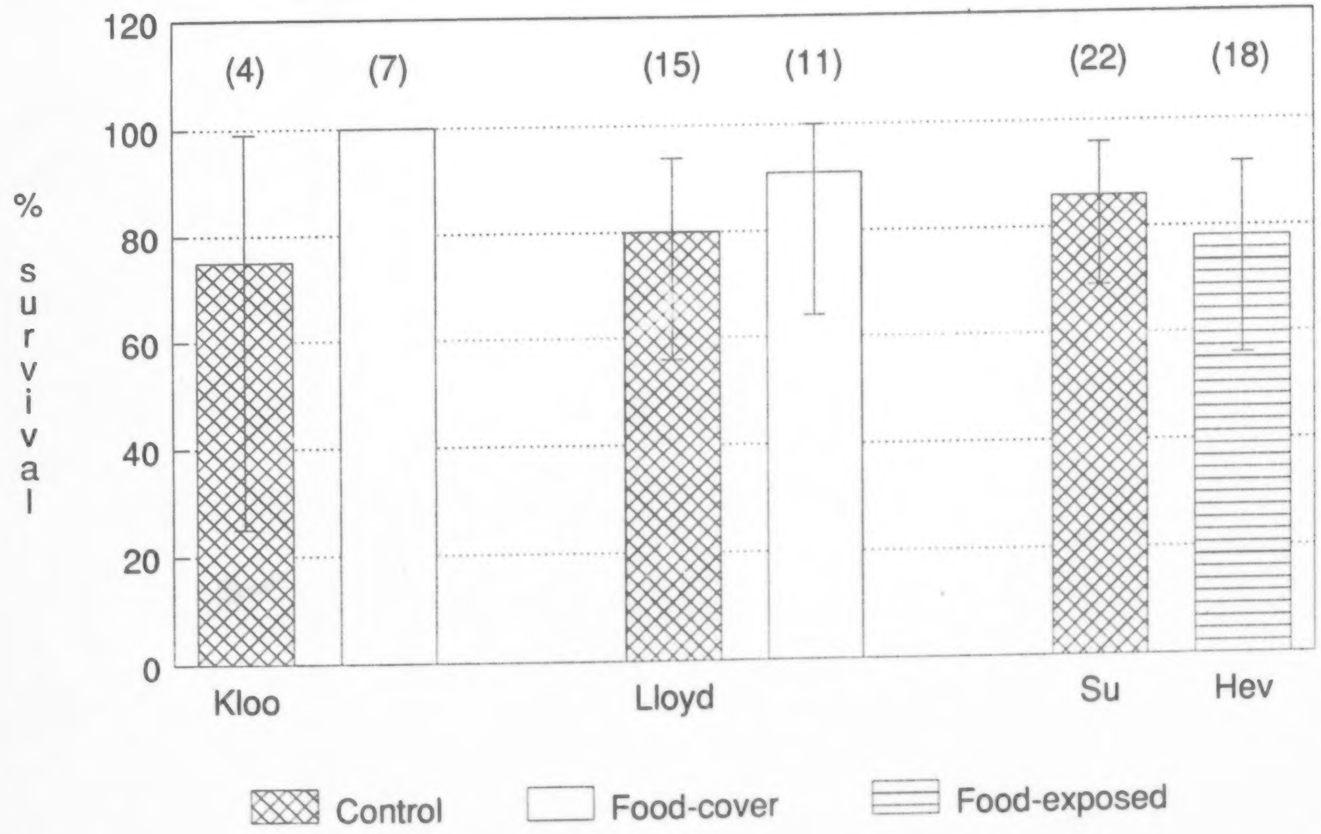

Figure 3.5. Survival of females from May through July 1991 on each site. Sample size in parentheses. Error bars calculated with the binomial approximation. No significant differences among sites or treatments.

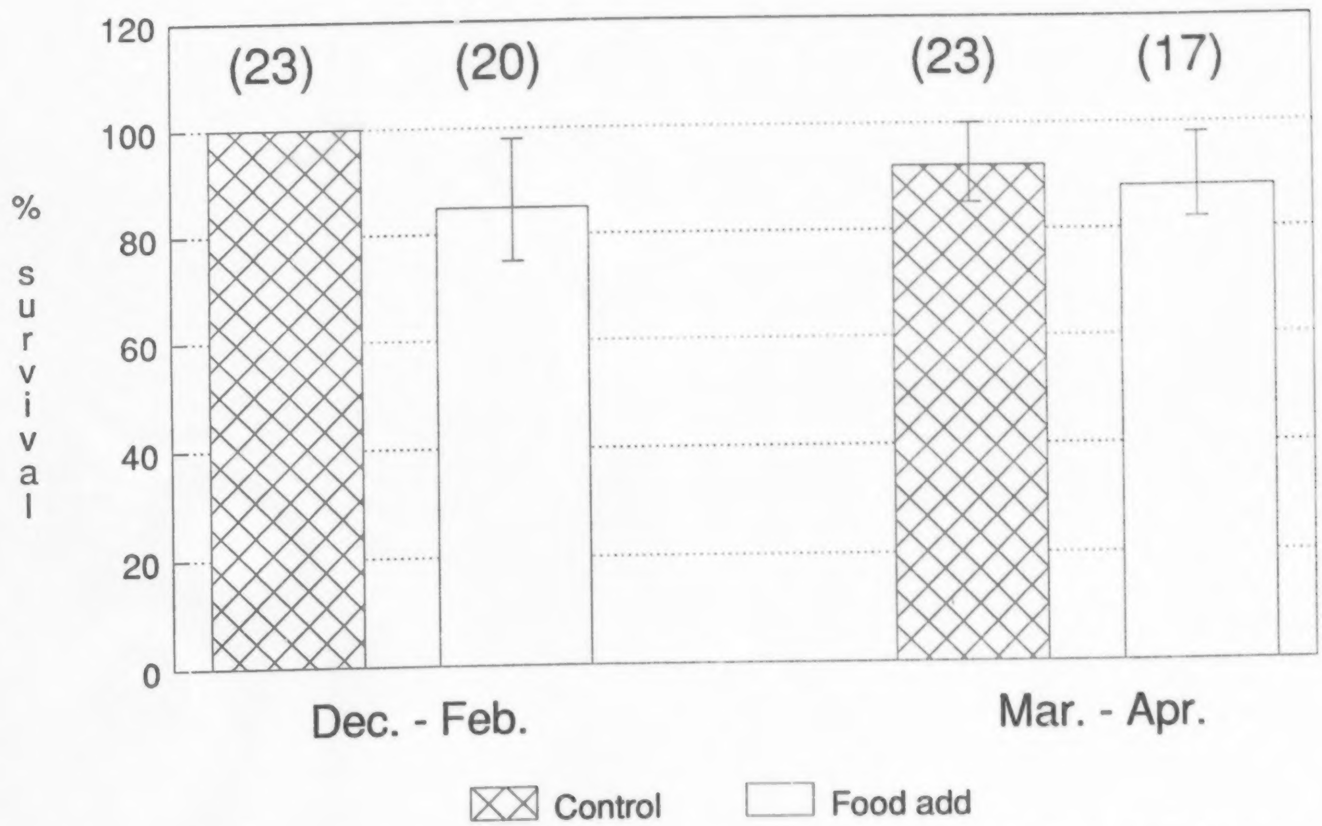

Figure 3.6. Survival of females given supplemental food and control females from December 1991 through February 1992 (G=2.43,p=.121) and from March through April 1992 (G=.42,p=.52). Sample size in parentheses, error bars calculated using the binomial approximation.

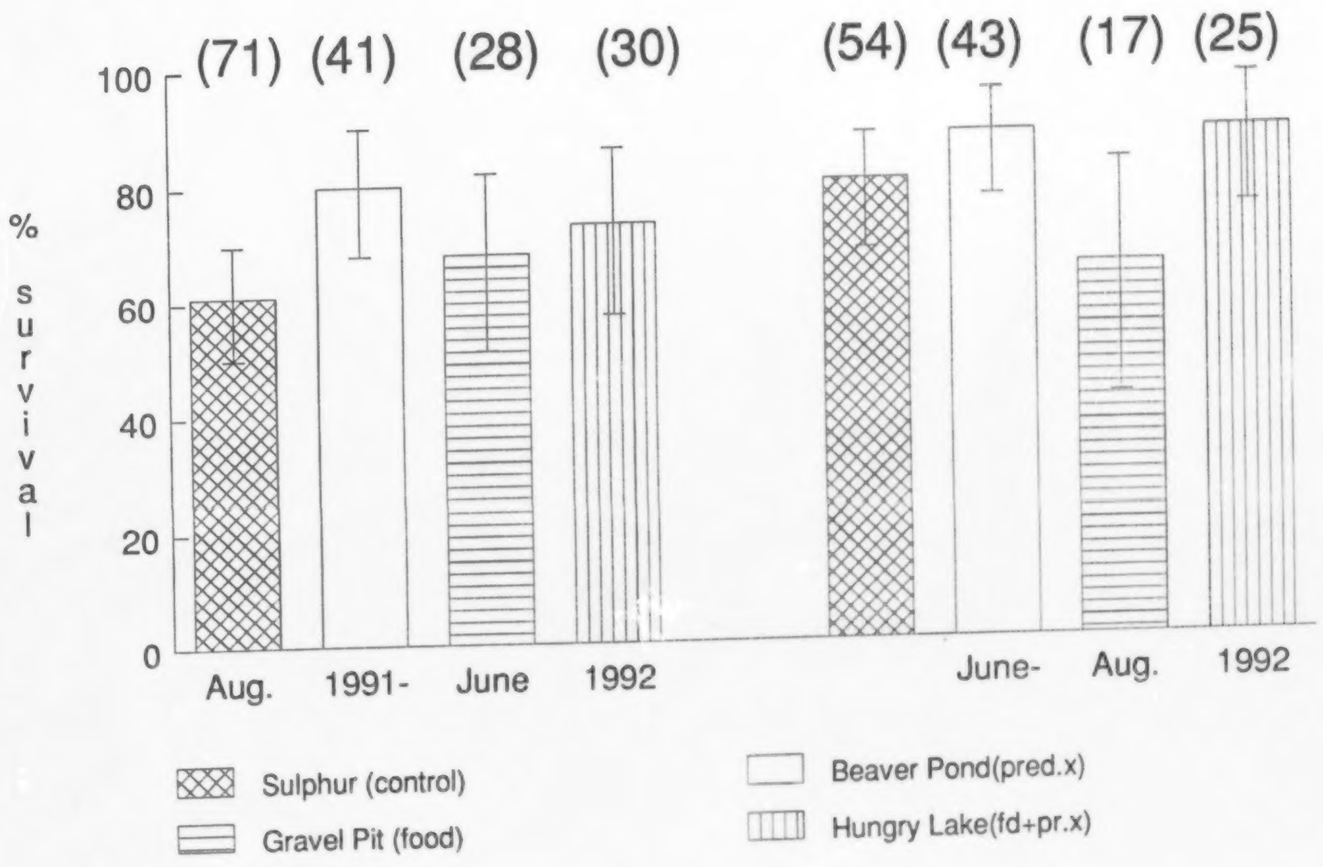

Figure 3.7. Survival of adults on each of the four sites used in experiment 3. Error bars calculated with the binomial approximation. Sample sizes in parentheses. No significant differences among sites.

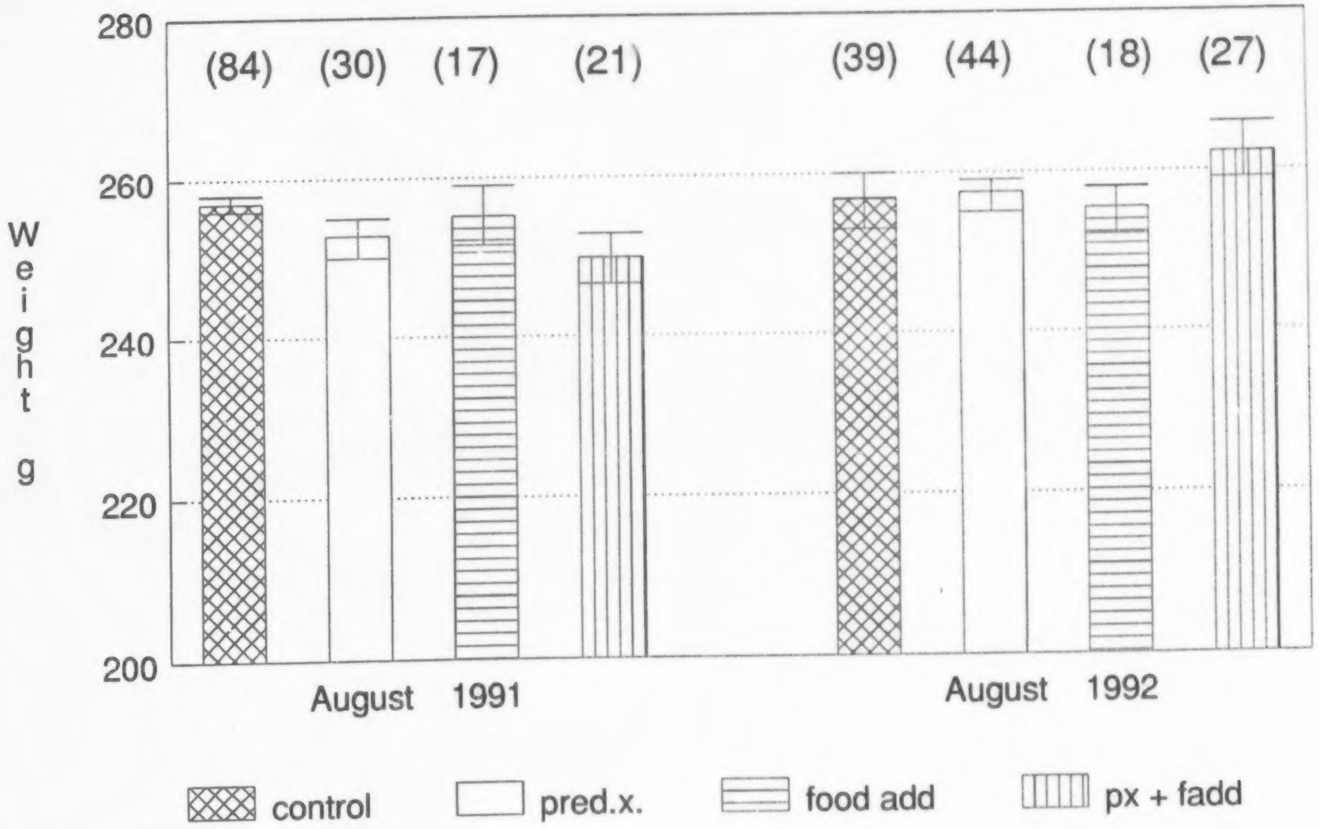

Figure 3.8. Average August body weights (and standard errors) of adults on each of the four sites used in experiment 3. No significant differences among sites.

FUTURE DIRECTIONS

Chapter 2 showed that predation on red squirrels can increase during a snowshoe hare decline, and that predation can cause a decline in red squirrel density. As such, this study supports one of the main predictions of the Alternative Prey Hypothesis (that predation on alternative prey should increase as main prey decline), and makes a strong contribution to the field of population ecology. Although this study provides evidence from only one snowshoe hare cycle, the experimental manipulation of predators strengthens conclusions considerably, and distinguishes this as the first such experimental study on an alternative prey species in North America.

This study monitored red squirrel populations only over two years of a snowshoe hare cycle, however, and thus cannot determine if red squirrels will recover from the decrease in density due to predation, or if they show 9-11 years population cycles similar to snowshoe hares. If red squirrel populations are limited ultimately by minimum territory size and thus the number of territories, as Klenner's (1991) work suggests, and if the probability of a juvenile surviving winter depends on the acquisition of a high quality territory, then high juvenile survival or recruitment over winter (due to a high number of juveniles acquiring adult territories vacated by predation) should be able to compensate for high adult mortality due to predation. Continued study of red squirrels in Kluane should provide the answer to this question. If red squirrels are found not to display population cycles, but rather maintain relatively stable populations over time, it would be of interest to compare red squirrels to other alternative prey to determine why they appear less vulnerable to predation.

The level of food does not appear to affect predation rates on adult red squirrels, as additions of food to individuals adults did not improve survival, either during summer or winter (Chapter 3). However, the level of food may only affect adult survival when very low, and food was not added at the critical time - May and early June 1992, when natural food levels may have been low, weather conditions harsh, and female mortality high - to assess this. The factorial experiment in Chapter 3 where predation and food were manipulated at the population level cannot be considered a strong test of the importance of food to adult survival, as it was not known whether or not red squirrels were eating the rabbit chow provided and squirrels on different sites may have obtained differing amounts of food. A useful experiment would be to remove food and measure predation on red squirrels.

Results from Chapter 3 suggest that the distribution of food does not play a major role in determining predation, and that the amount of time a red squirrel spends exposed to predators while foraging is not an important component of predation risk. This result may only hold under the level of predation during the experiment, which was not high. At higher levels of predation pressure, as were observed in 1992, the outcome to this experiment may have been different. However, the experiment still prompts some interesting questions. What is the most important component of predation risk for red squirrels, and during what behaviour are squirrels at the highest risk ? Or do factors other than behaviour have a stronger influence on predation risk ? Factors associated with an individual's territory such as the location with respect to habitat edges (Stuart-Smith, unpubl. data) or the density of trees (Larsen 1992), may determine predation risk to a higher degree than behaviour. Determining the important components of predation risk may shed light on some aspects of red squirrel behaviour. As 'few failures are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness' (Lima and Dill 1990), it is likely that squirrels perceive and adjust their behaviour according to the prevailing predation risk. I showed in Chapter 3 that supplemental food can be used to manipulate individual red squirrel behaviour, and future studies could use food to manipulate different behaviours under controlled levels of predation risk. It would also be useful to perform further factorial manipulations of food and predation with a high quality food such as sunflower seeds, and measure variables such as foraging behaviour, vigilance, growth rates, and predation. Food and predation may have interactive effects on these variables, as other studies (Desy and Batzli 1989; Desy *et al.* 1990) have shown for voles.

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APPENDIX I

SNOWSHOE HARE DENSITIES

Data presented in this and the following appendices is taken from the most recent Annual Report of the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* unpubl.) and from unpublished reports compiled by F. Doyle.

Snowshoe hares (*Lepus americanus*) are live-trapped on each of the nine main study sites at least four times per year. Each trapping session is conducted over two days at 86 permanent trap stations (at grid stakes) per site. The Jolly-Seber model is used to estimate density. Figure I.1 shows the trend in hare densities on the four main sites used in my study, Sulphur (control), Beaver Pond (predator exclosure), Gravel Pit (food addition), and Hungry Lake (predator exclosure plus food addition) from 1986 to 1992. Hare densities on Lloyd, another control site I used, followed a similar trend to densities on Sulphur. Populations of hares have been increasing since 1986, reached peak densities in 1989-1990, and began to decline in 1991. The 'crash' occurred during the winter of 1991-92, when densities on Sulphur and Beaver Pond declined 77 % and 71 % respectively. Densities on Sulphur declined a further 50 % from March 92 to October 92. The highest densities were reached on Gravel Pit and Hungry Lake in October 1990, and hare populations on these sites declined somewhat later than those on other sites.

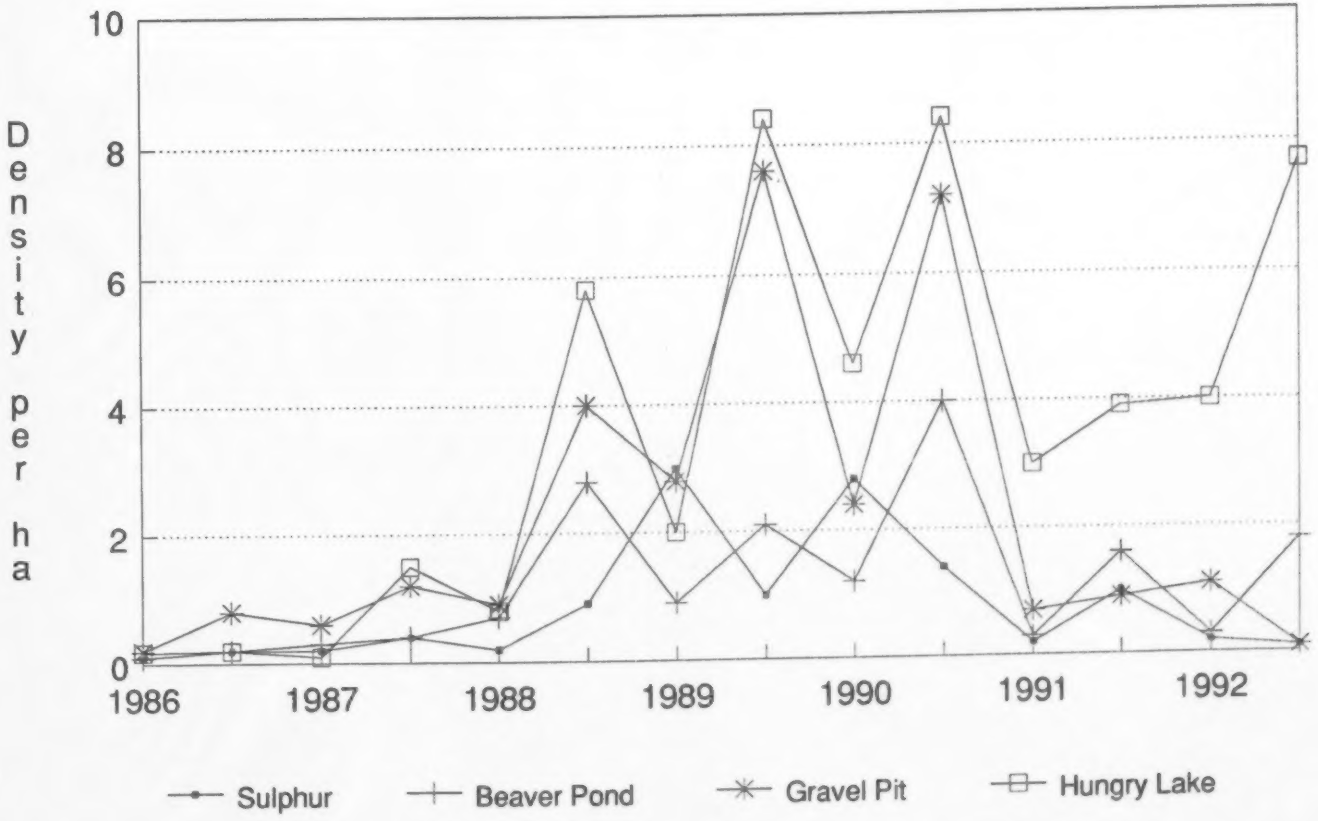

Figure I.1. Trends in snowshoe hare densities on four main study sites at Kluane from 1986 through 1992.

APPENDIX II

PREDATOR DENSITIES AND DIETS

Mammalian Predators

Lynx (*Lynx canadensis*) and coyote (*Canis latrans*) are the principal mammalian predators in the Shakwak valley. Their numbers are estimated through a combination of live-trapping, home range analysis, howl surveys (coyotes only) and winter track counts. Trends in numbers can most easily be seen in the track counts, which are thought to approximately parallel actual numbers of animals. Tracks have been counted since winter 1986-87 along a series of snowmobile trails running the length of the study area. Track counts of both predators have generally increased since winter 1986-87, reached peak numbers in winter 1991-92, and declined in winter 1992-1993 (Figure II.1). Since 1986, lynx tracks have increased 9-fold and coyote tracks 11-fold. The two years of my study thus corresponded with peak densities of these two predators.

Winter track counts also showed Red fox, wolf, weasel, and wolverine present in the area, but at very low densities (Figure II.2) and with no obvious correlation with the trend in hare densities. Martins have been seen is the study area, but very rarely with the last sighting in March 1990. Weasels, the only predator able to obtain access to red squirrel nests in Kluane due to their small size, showed fewer than 5 tracks per 100 km in 1991-91, and fewer than 7 per 100 km in 1991-92. The large increase in 1992-93 is likely due to the high density of voles in summer 1992 (C.J. Krebs, unpubl. data).

Dietary composition of lynx and coyote was determined by scat analysis. Prey remains in scats were quantified by frequency of occurrence in 10 sub-samples from each scat and grouped into four items: hares, rodents (voles and mice), sciurids (ground and red squirrels) and other (grouse, small birds etc.). It is possible to distinguish between red and ground squirrels in the winter diet, however, as only red squirrels are available prey in the winter months. A general increase in the percent occurrence of hare is seen in the diet of both predators from 1988 to peak hare densities in 1989-1990 (Figure II.3a,b). However, hares still formed almost all of the diet of both predators in winter 1990 and winter 1991-92, despite the decline of the hares in 1991-92. Hares generally composed a greater part of the diet of lynx (Figure II.3a) than of coyote, although coyotes were heavily dependant on hare in the winters (Figure II.3b). Sciurids were eaten mainly in the summers. Unfortunately, data for summer 1992, when I observed substantial predation on red squirrels, is not yet available.

Avian predators

The total breeding population of raptors has been censused within a 100 km^2 intensive area extending from Kluane Lake to the Hungry Lake site since 1989. Data in Table II.1 only represent breeding pairs, numbers of non-breeders or floaters are unknown. Thus these data must be considered minimum numbers only. All sightings of raptors in the study area are recorded, and this data presumably reflects numbers of both breeders and non-breeders. However, sighting counts were not available for all raptors in all years, and show may peaks due to a migration of birds passing through the area or to an increase in hunting activity of the resident birds as food becomes scarce. Thus, breeding counts were used. Northern goshawks (*Accipiter gentilis*) and Harlan's hawks (*Buteo harlanii*), for whom both types of data are available, show similar trends in both sets of data. The most common avian predators are the resident great horned owls (*Bubo virginianus*) and the migratory Harlan's hawks, although northern goshawks may be more common than estimated. Numbers of breeding large raptors generally increased from 1989 to 1990, but remained stable from 1991 to 1992 (Table II.1). Breeding success of all raptors except the Harlan's hawk peaked in 1990, declined in 1991, and almost failed completely in 1992 (Table II.1). Breeding success of Harlan's hawks remained stable from 1989 through 1991, but declined in 1992. This may reflect a diet not as dependant on hares as the other raptors. Unfortunately, data on diet composition is limited for the raptors, but goshawks and Harlan's hawks are thought to take more red squirrels than the other raptors (F. Doyle, pers. comm.).

Species	Year	Breeding pairs in 100^2 km	Young fledged per pair (N)
Great horned owl	1989	14-16	2.2 (15)
	1990	19	2.3 (20)
	1991	22	1.4 (19)
	1992	23-25	0 ? (?)
Northern goshawk	1989	1-2 (min)	1.3 (3)
	1990	5	3.8 (11)
	1991	3	1.3 (3)
	1992	3	0.0 (1)
Harlan's Hawk	1989	7-9	1.0 (5)
	1990	10	1.0 (10)
	1991	11	1.0 (5)
	1992	12	0.4 (16)
Northern harrier	1989	1-2 (min)	4.0 (1)
	1990	4	4.0 (3)
	1991	4	2.6 (5)
	1992	3	3.3 (3)
Bald eagle	1989	1	0.5 (2)
	1990	1	0.5 (2)
	1991	1	1.0 (2)
	1992	1	0.0 (2)
Northern hawk owl	1989	1-2	3-4 (1)
	1990	4	4.0 (3)
	1991	1	0.0 (1)
	1992	0	0.0 (0)
Total raptors	**1989**	**25-31**	
	1990	**43**	
	1991	**42**	
	1992	**42-44**	

Table II.1. Numbers of breeding pairs of raptors in the 100 km^2 intensive area in the Shakwak valley, and the average number of young fledged per pair (sample size in parentheses), from 1989 to 1992.

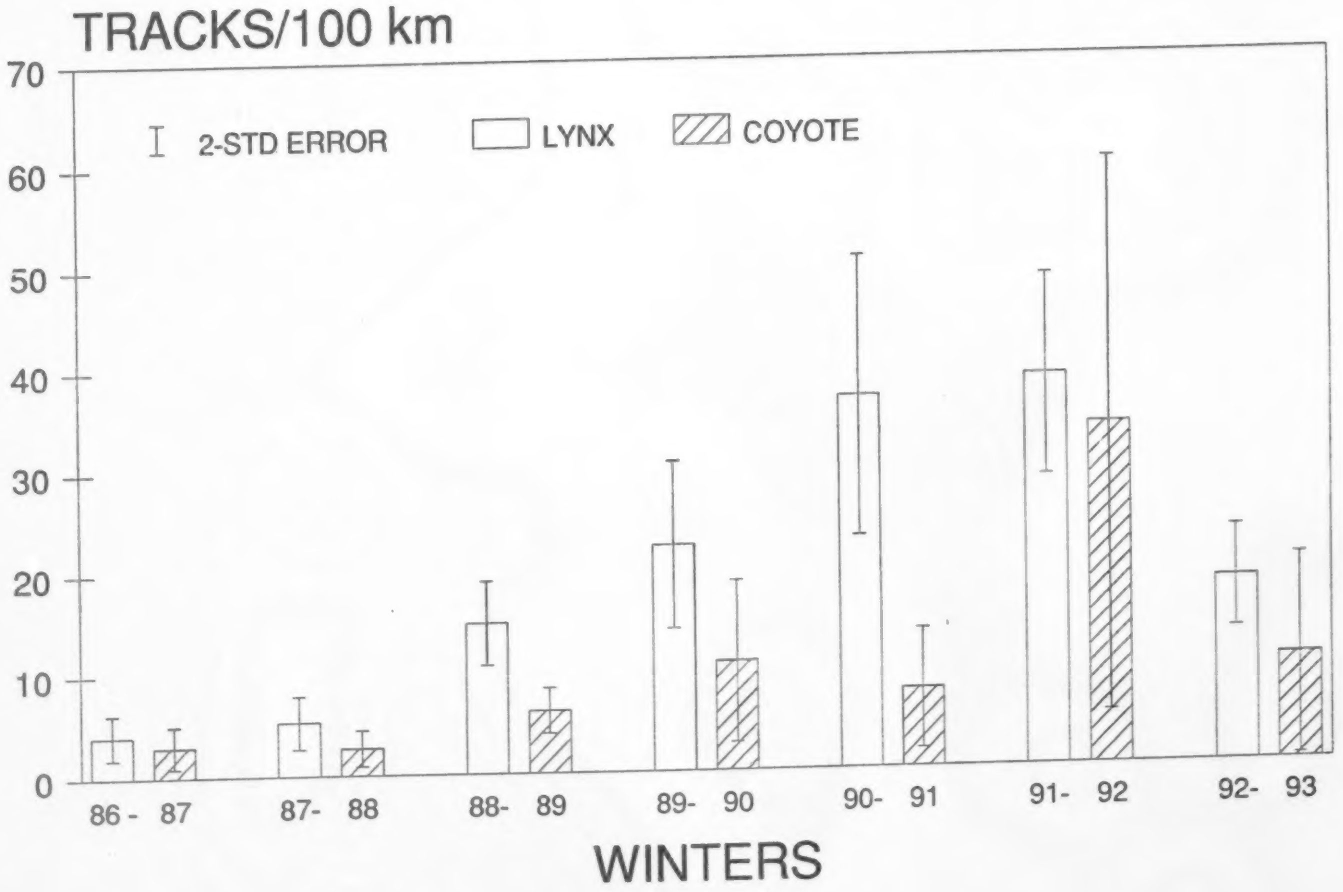

Figure II.1. The number of lynx and coyote tracks per 100 km in Kluane, each winter from 1986-87 through 1992-93.

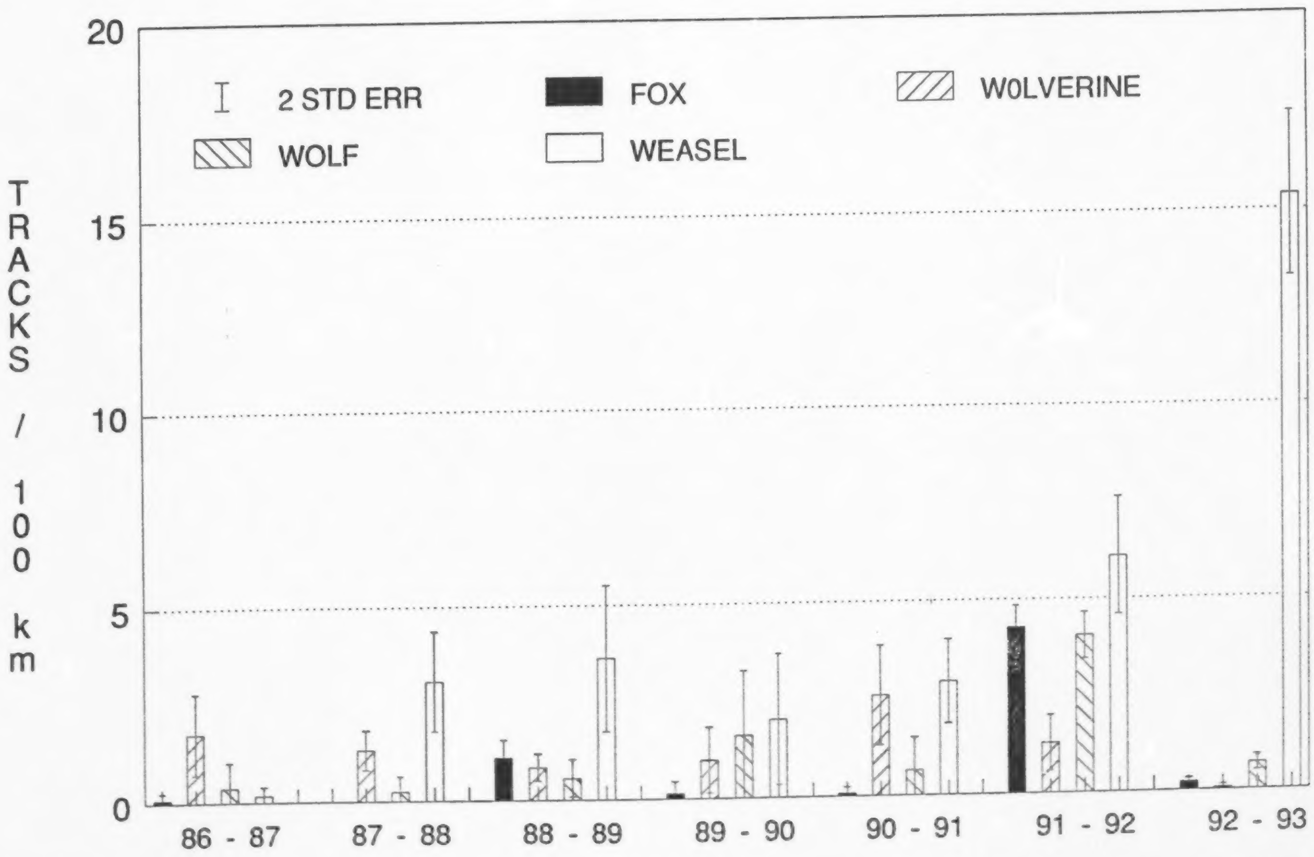

Figure II.2. The number of wolf, fox, weasel, and wolverine tracks per 100 km in Kluane each winter from 1986-87 through 1992-93.

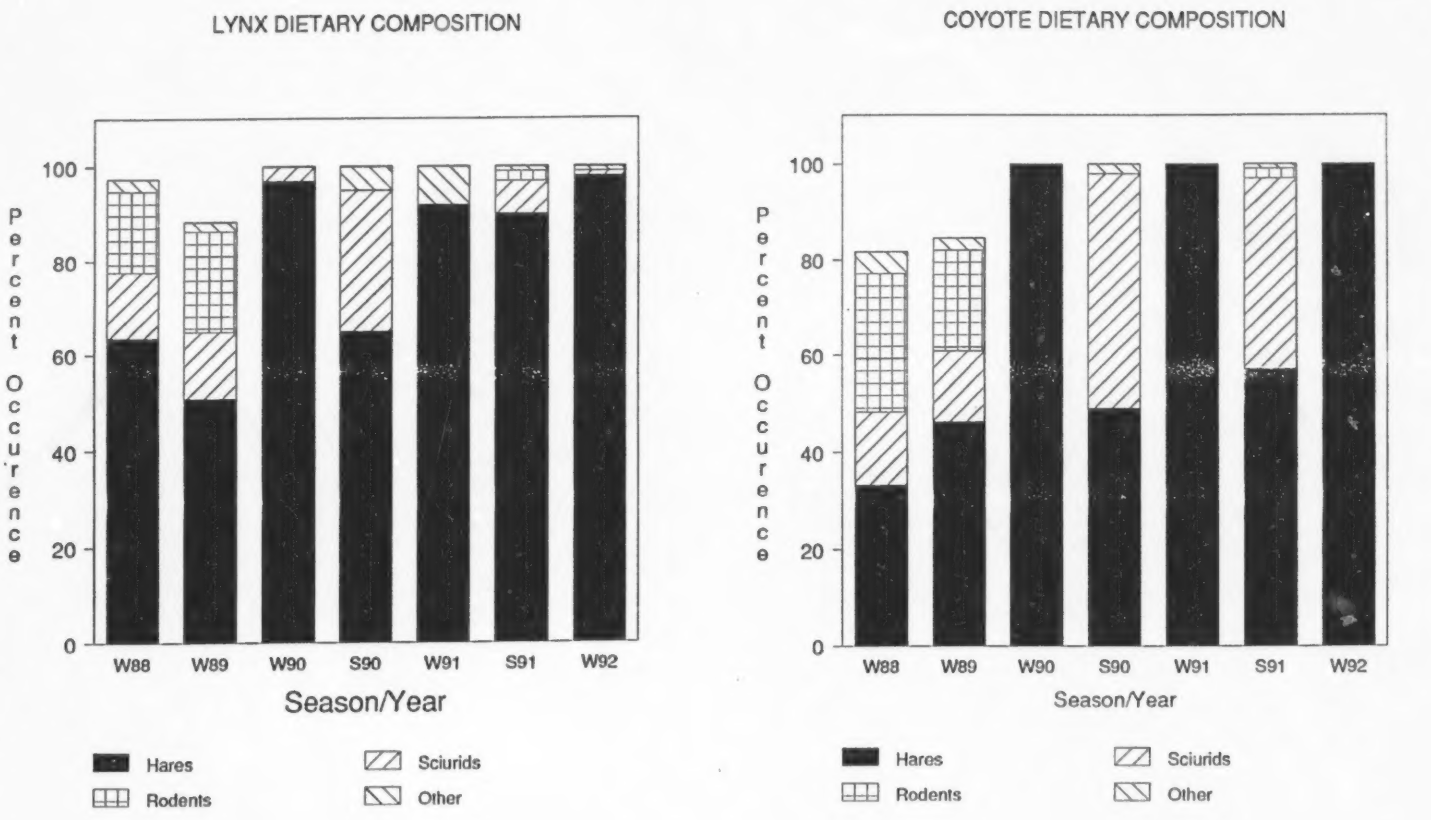

Figure II.3 The percent occurrence of various prey groups in the diet of lynx (Figure II-3a) and coyote (Figure II-3b) at Kluane from winter 87-88 (W88) to winter 1991-92 (W92).

APPENDIX III

KLUANE HERBIVORE BIOMASS PYRAMID

Herbivore biomass pyramids were constructed from the average weight (obtained from Kluane data) and the density per 100 sq. km in the breeding season (extrapolated from Kluane density estimates) for each herbivore. Data are only available for 1987 through 1990, but Figure III.1 shows red squirrels to have the second highest biomass after hares in all years, with the exception of 1990 when ground squirrel densities were high. Changes in the relative biomass of red squirrels with changing hare densities are also evident, with red squirrels composing about 25 % of the herbivore biomass in 1987 when hares were at low densities, and about 12 % in 1989 when hares were at their peak densities.

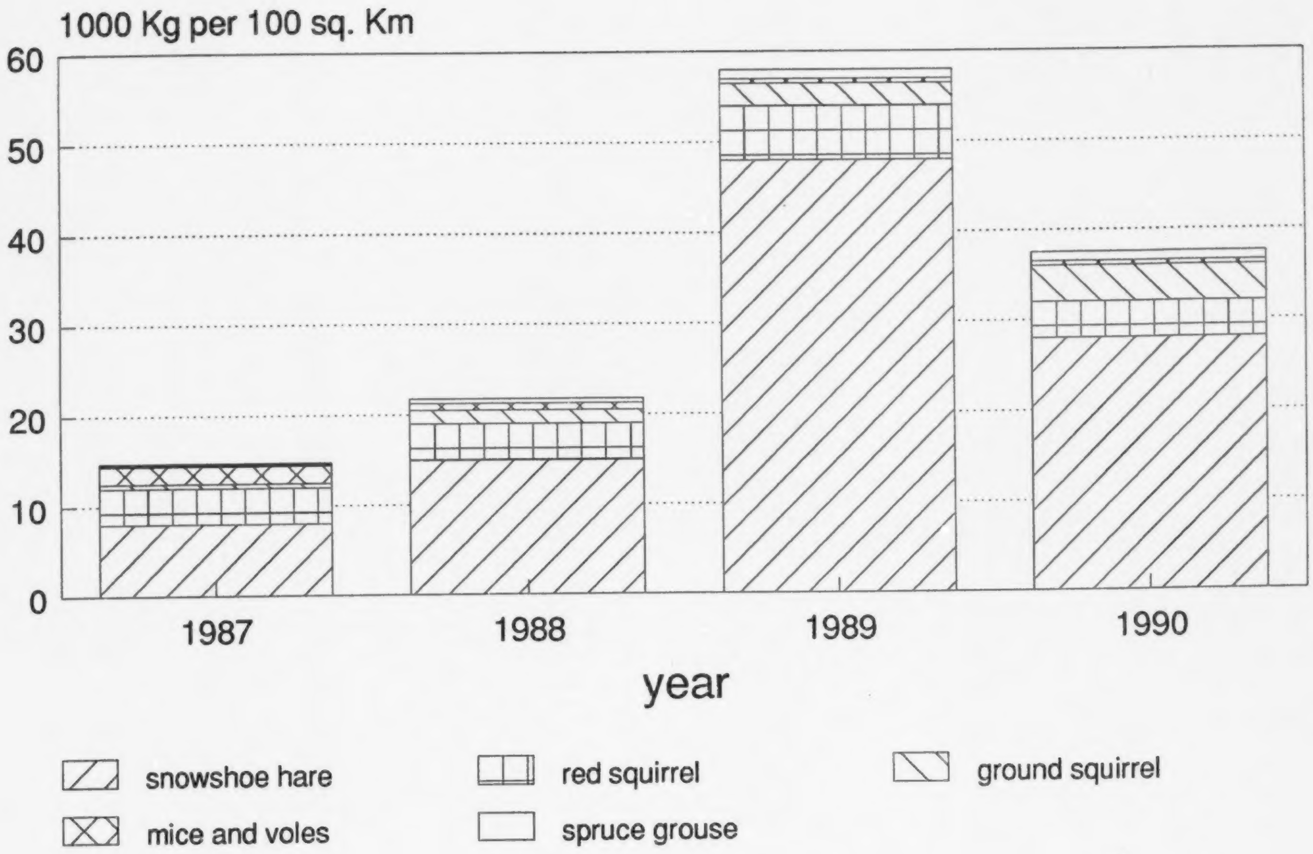

Figure III.1. Herbivore biomass pyramid for the main herbivores at Kluane. See text for methods of calculation.

APPENDIX IV

CONE PRODUCTION

White spruce cone production has been measured in Kluane study area each August since 1986. Cones are counted on each study site in early August following maturation of the cones and before much harvesting by red squirrels has taken place. Using binoculars, the number of cones in the top 3 meters on each of 86 trees on each site is counted (the same trees are used each year). If the number exceeds 100, a photograph is taken and the cones later counted on the print. The average number of cones per tree does vary slightly between sites, but it is difficult to determine how large this variation has to be before it significantly affects red squirrel demographics. In addition, inter-site variation is likely less than inter-year variation (S. Boutin, pers. comm.). Thus, data for all sites were combined and are presented for the entire study area. Although my study was conducted from 1991 through 1992, cone production in 1990 is important as cones maturing then formed the basis of the squirrels food cache during winter 1990-91 and spring 1991. Cone production during this study varied substantially, with the majority of trees bearing many cones in 1990 and 1992, but virtually no trees producing any cones in 1991 (Figure IV.1). The cone crop in 1992 was the highest in the region since 1988. Cones from this crop would have been present on the trees as immature cone buds in winter 1991-92, and as such may have formed an abundant food source for squirrels during this winter when few mature cones were available (due to the cone failure in 1991).

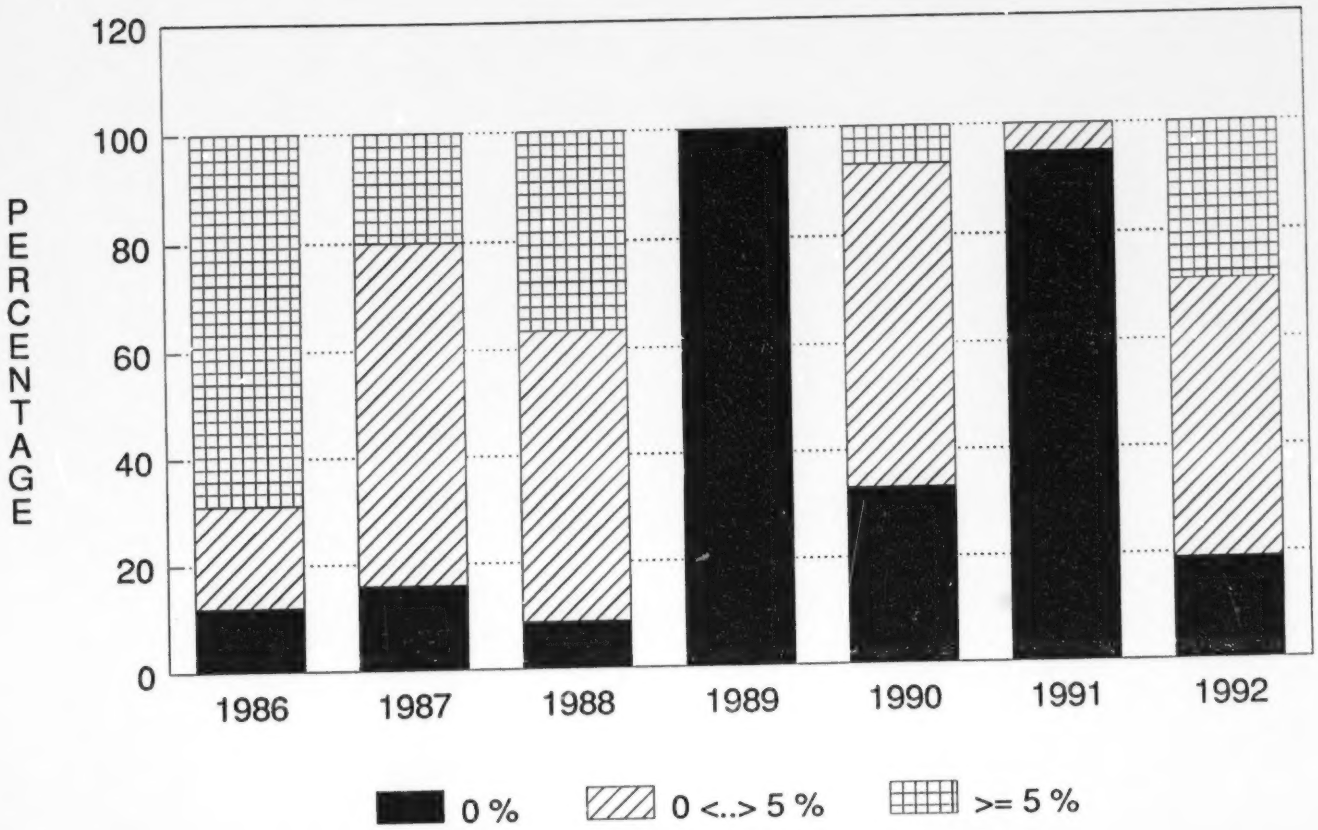

Figure IV.1. The percent of white spruce trees bearing cones in each of three categories of cone cover. Data pooled from samples of 86 trees on each of 9 sites.